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Un nouveau *Leptodactylodon* de la Dorsale camerounaise (Amphibia, Anura)

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A new species of *Leptodactylodon* is described from montane forest in the Bakossi Mounts (Cameroun). This species is in the complex of small *Leptodactylodon* with well-developed vomerine teeth. Its specific characters include very small size, narrow head, males without gular folds and spiny skin, but with rather thick front legs. The voice is highly characteristic, as the main calls are reminiscent of the noise produced by the cords of a guitar being plucked.

Le pôle de diversification maximale des Astylosterninae Noble, 1927 se situe au Cameroun, et plus précisément dans la partie occidentale du territoire, où se dressent les montagnes et les plateaux de la Dorsale camerounaise. Les cinq genres de la sous-famille y sont représentés et, parmi eux, les genres *Astylosternus* Werner, 1898 et *Leptodactylodon* Andersson, 1903 comprennent chacun une dizaine d'espèces, pour la plupart orophiles (AMIET, 1977, 1980).

Pour ces deux genres, les variations climatiques quaternaires, en entraînant d'importants changements dans les limites altitudinales des étages, et donc des extensions ou des morcellements des aires de répartition, ont eu pour corollaire la formation d'espèces qui peuvent être étroitement localisées (AMIET, 1975, 1987).

C'est probablement le cas pour le *Leptodactylodon* décrit ici. Cette espèce, trouvée uniquement près des villages de Kodmin et d'Edib, dans les Monts Bakossi, était restée ignorée malgré les prospections répétées effectuées par l'un de nous (JLA) sur le Mont Manengouba, à une dizaine de kilomètres à vol d'oiseau de la première localité. Elle a été découverte grâce à ses vocalisations, enregistrées en marge de recherches ornithologiques (FDL): soumises pour identification, il apparut immédiatement qu'elles étaient produites par

une espèce encore inconnue. Toutefois, leurs caractéristiques acoustiques étaient si inhabituelles qu'il ne fut même pas possible d'imaginer à quel genre leur auteur pouvait appartenir !

Aucun spécimen n'avait été récolté, mais l'emplacement d'un groupe de mâles vocalement actifs avait été bien repéré. Chris Wild, alors coordinateur scientifique des projets Kupe-Bakossi-Takamanda (WWF Cameroun), put ainsi, à notre demande, y faire rechercher cette espèce. Grâce à la collaboration de D. Menze et E. Abwe, 6 mâles et un juvénile purent être capturés en décembre 1998. Ce matériel nous permet de décrire une nouvelle espèce que nous sommes heureux de dédier à C. Wild, qui a contribué à résoudre l'énigme posée par ses appels.

Remarques méthodologiques

(1) Dans les montagnes camerounaises, de nombreuses espèces d'anoures ont, comme les *Leptodactylodon*, une activité vocale diurne (Amiet, 1989). Nous reproduisons ci-après le passage d'une lettre de C. Wild (lettre du 21 janvier 1999 à JLA) décrivant le procédé qu'il a utilisé pour séparer auditivement la nouvelle espèce de celles qui lui étaient associées: "(...) the site was marked off with tape (about 5 m × 5 m), left undisturbed, and revisited (...) for intensive microhabitat search involving the removal of all vegetation and debris. Forty two (42) anurans were captured, comprising: *Phrynobatrachus*, *Phrynodon*, *Wolterstorffina*, *Arthroleptis* and some small '*Leptodactylodon*-like' specimens. All were brought back to my house in Nyasoso and placed in a large container covered in muslim mesh with vegetation. Within 24 hours the 'guitar' calls were heard. I then isolated the group by species to identify which type was calling. Within the next 24 hours, the group calling with the exact same guitar-like voices was conclusively determined."

(2) Ainsi que l'un de nous l'a déjà souligné (Amiet, 1980), les rapports morphométriques sont rarement discriminants chez les *Leptodactylodon*. Les quelques mensurations données ici (tab. 1-2), ainsi que leurs abréviations, seront les mêmes que dans la "Révision" précitée : L, longueur du corps, mesurée de l'extrémité du museau à l'entrejambe; T, largeur de la tête derrière les yeux ; C, longueur de la cuisse, de l'entrejambe au genou ; J, longueur de la jambe, de la saillie du genou à celle du talon ; P, longueur du pied, du talon à l'extrémité de l'orteil 4.

Leptodactylodon wildi n. sp.

Matériel étudié.

Holotype. – Mâle MNHN 2000.0607 de Kodmin (Cameroun, env. 1350 m), décembre 1998, C. Wild leg. Individu en livrée nuptiale (épines métacarpiennes bien développées). Habitus : voir fig. 1. Mensurations: voir tab. 1.

Paratypes. – 5 mâles en livrée nuptiale de même origine, capturés avec l'holotype et déposés aux muséums de Paris (MNHN 2000.0608-0610), Bonn (ZFMK 72150) et Londres (BMNH 1998.382).

Tab. 1. – Quelques mensurations (en dixièmes de mm) et proportions chez *L. wildi*. L'holotype est le spécimen MNHN 2000.0607.

N° spécimen	L	T	C	J	P	T/L	C/L	J/L	P/L
MNHN 2000.0607	225	85	90	85	140	37,8	40	37,8	62,2
MNHN 2000.0608	230	85	80	90	150	37	34,8	39	65,2
MNHN 2000.0609	215	80	85	80	135	37,2	39,5	37,2	62,8
MNHN 2000.0610	235	85	85	95	140	36,2	36,2	40,4	59,6
BMNH 1998.382	225	80	85	95	140	35,5	37,8	42,2	62,2
ZFMK 72150	235	80	85	95	135	34	36,2	40,4	57,4
Moyenne	230	82,5	87,5	90	140	36,28	37,42	39,50	61,57
Ecart-type	7,58	2,74	3,16	6,32	5,48	1,38	2,05	1,86	2,71

Tab. 2. – Données morphométriques relatives aux *Leptodactylodon* proches de *L. wildi*. Ep. métac. : nombre d'épines métacarpiennes. Les données concernant les espèces autres que *L. wildi* sont extraites de AMIET (1980).

Espèce (nombre de spécimens)	L	T/L	J/L	P/L	Ep. métac.
***L. albiventris* (9)**	25,7	36,8	41,6	63,5	2
***L. bueanus* (6)**	26	37,9	43,9	64,2	3
***L. p. polyacanthus* (7)**	25,2	38,8	43,8	66	5-6(7)
***L. p. punctiventris* (7)**	25,2	38,7	44,1	64,8	5-6
***L. wildi* (6)**	23	36,2	39,5	61,5	4

Autre matériel. – (1) Un juvénile de même origine; (2) trois diapositives C. Wild de spécimens vivants ou fraîchement sacrifiés ; (3) deux enregistrements sonores F. Dowsett-Lemaire, effectués à Kodmin en mars-avril et décembre 1998.

Diagnose. – *Leptodactylodon wildi* se rapproche de *L. albiventris* (Boulenger, 1905) et *L. polyacanthus* Amiet, 1971 par ses dents vomériennes en courtes crêtes transverses, sa face ventrale non marbrée et sa taille inférieure à 30 mm. Il s'en distingue par sa taille plus faible (21,5 à 23,5 mm chez les mâles), par sa tête plus étroite, et surtout par les caractères sexuels secondaires du mâle : bras hypertrophiés (différence avec *L. albiventris*), épines métacarpiennes au nombre de 4, absence de plis gulaires (différence avec *L. albiventris*) et de spinosité pectorale (différence avec *L. polyacanthus*). Il se sépare aussi de ces espèces par divers traits de coloration, et de toutes les autres espèces de *Leptodactylodon* par ses vocalisations.

Description.

Habitus, tégument, membres. – *L. wildi* (fig. 1 et 4) est une des plus petites espèces du genre: les six mâles récoltés, adultes comme le montre le développement de leurs caractères sexuels, mesurent de 21,5 à 23,5 mm, ce qui les situe dans le même ordre de grandeur que *L. bicolor* Amiet, 1971, *L. mertensi* Perret, 1959, *L. erythrogaster* Amiet, 1971 et *L. perreti* Amiet, 1971. Comme ces derniers, il a une forme générale plutôt cylindrique, avec les flancs longuement parallèles, mais il s'en sépare à première vue par sa tête relativement étroite (T/L de l'ordre de 36 % : tab. 1) et par ses membres postérieurs encore plus courts et plus épais (fig. 2). Cet habitus le distingue aussi d'un petit *Leptodactylodon* gabonais, *L. blanci* Ohler, 1999, dont la tête est large et la forme plus trapue (Ohler, 1999: fig. 1).

Chez les individus étudiés, le tégument dorsal paraît lisse, ce qui pourrait être dû, au moins en partie, au mode de fixation (ces spécimens étaient légèrement gonflés). Les photos de C. Wild, prises sur le vivant ou sur des spécimens récemment sacrifiés, confirment que le relief tégumentaire se limite à de vagues rides ou verrucosités à peine perceptibles, surtout sur les côtés du corps.

Le museau est largement arrondi et dépourvu de canthus et de dépression loréale, contrairement à ce qui s'observe chez *L. albiventris* et *L. polyacanthus*. Les narines ne sont marquées par aucun relief ; elles se trouvent un peu plus près de l'extrémité du museau que des angles palpébraux antérieurs. Les yeux, comme chez tous les *Leptodactylodon*, sont relativement petits et peu saillants ; ils sont largement séparés, l'espace interoculaire représentant environ 1,5 fois la plus grande largeur de la paupière (sur la tête vue en plan). Le tympan est indiscernable, peut-être en raison du gonflement des spécimens, mais un faible repli supratympanique est visible.

La main (fig. 3b) présente les caractères habituels chez les *Leptodactylodon*, avec des doigts courts se rétrécissant régulièrement vers leur extrémité, qui est à peine élargie. Le doigt 1 est plus long que le doigt 2. Il y a deux tubercules sous-articulaires aux doigts 4 et 3, et un aux doigts 2 et 1 ; à chacun des doigts, les tubercules proximaux forment de larges coussinets peu saillants. La paume présente deux plages d'aspect semblable, l'une externe, plus ou moins dédoublée, l'autre interne, prolongeant la saillie où sont implantées les épines métacarpiennes du mâle.

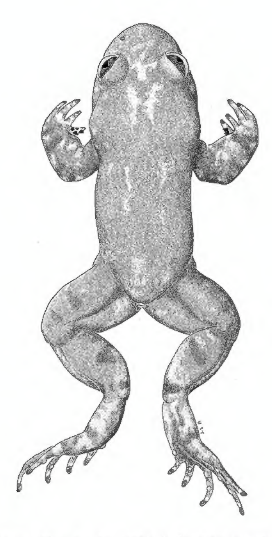


Fig. 1. – *Leptodactylodon wildi* n. sp., face dorsale de l'holotype, MNHN 2000.0607, de Kodmin (Cameroun), 21.XII.98, Wild leg. (dessiné après fixation).

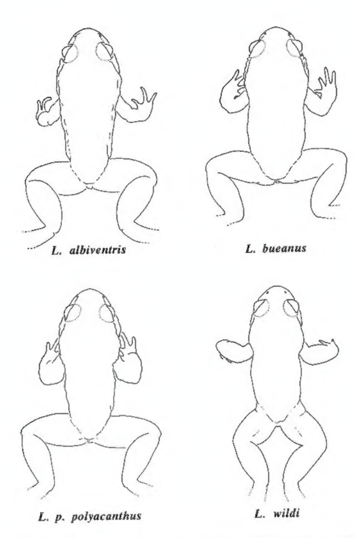


Fig. 2. – Habitus des petits *Leptodactylodon* à dents vomériennes développées. *L. albiventris*, JLA 70.975, de Wom ; *L. bueanus*, JLA 78.155, de Bolifamba ; *L. p. polyacanthus*, JLA 70.941, de Bafut-Ngemba ; *L. wildi*, MNHN 2000.0608, de Kodmin. Remarquer la forme de la tête chez *L. wildi*.

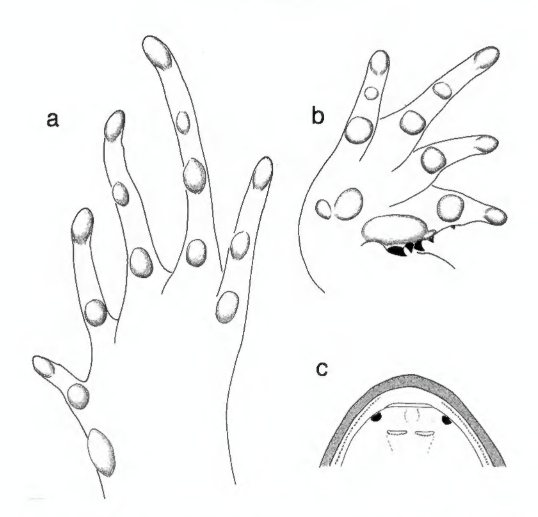


Fig. 3. – *Leptodactylodon wildi* : a, pied, face plantaire ; b, main, face palmaire ; c, plafond de la cavité buccale montrant la disposition des dents vomériennes.

Les membres postérieurs sont encore plus courts que chez les autres *Leptodactylodon*, avec des cuisses volumineuses, presque ovoïdes. Les pieds (fig. 3a) sont larges et épais et portent des orteils qui paraissent largement séparés à leur base car ils sont assez minces et dépourvus de toute palmure interdigitale. Leurs extrémités sont faiblement dilatées ; les tubercules sous-articulaires, peu saillants, sont au nombre de trois à l'orteil 4, de deux aux orteils 3 et 5 et de un aux orteils 1 et 2. Il y a un tubercule métatarsien interne ovoïde, relativement petit mais un peu plus saillant que les tubercules sous-articulaires.

Livrée. – C. Wild a photographié un individu vivant (fig. 4) et deux individus fraîchement sacrifiés, ce qui permet de connaître la coloration de cette espèce in vivo.



Fig. 4. – *Leptodactylodon wildi* en vie (photo C. Wild). Remarquer la maculation céphalique caractéristique et l'épaisseur des membres postérieurs.

La face dorsale, moins foncée que chez *L. polyacanthus*, est brunâtre avec des marbrures beige olivâtre et quelques taches d'un jaunâtre terne. Ces dernières dessinent un motif céphalique caractéristique, bien visible même chez les individus fixés, comprenant : (1) sur le museau, une tache à contour irrégulier, de forme variable ; (2) une large bande interoculaire avec une dilatation médiane postérieure ; (3) deux bandes partant des yeux et convergeant vers l'arrière en direction de la région scapulaire en dessinant un X ou un Y ouvert vers l'avant ; toutes ces macules, mal circonscrites, ont un contour très diffus mais ressortent cependant bien sur la teinte foncière. L'iris est piqueté d'argent sur un fond brun-noir. Sur le reste du corps, quelques vagues macules jaunâtres se répartissent plus ou moins suivant deux lignes latéro-dorsales (caractère chromatique pouvant se retrouver chez *L. axillaris* Amiet, 1971).

Le dessus des membres antérieurs, la région coccygienne, les talons, la face antérieure des jambes et le dessus des pieds sont d'un jaune fauve terne, avec des traces de bandes transverses incomplètes sur les cuisses et les jambes.

La région gulaire, brune, est piquetée de quelques gros points subcirculaires d'un blanc bleuté, semblables à ceux de *L. polyacanthus* et *L. albiventris*. La coloration foncière de la poitrine et de l'abdomen est d'un blanchâtre un peu translucide, fortement suffusé d'un voile de chromatophores foncés. Le dessous des membres est d'un jaunâtre fauve, avec de petites macules diffuses brunes sous les bras et les cuisses, et de larges macules nébuleuses foncées sous les jambes et les pieds.

Caractères sexuels secondaires (1) Epines nuptiales. – La présence chez les mâles en livrée nuptiale de deux groupes d'épines coniques, noires, sur la tranche interne de la main et sur le doigt 1 représente un caractère générique des *Leptodactylodon* (AMIET, 1980). Chez *L. wildi*, le groupe distal comprend 4 épines (5 à une main chez deux individus), comme chez toutes les autres espèces. Le groupe proximal ("épines métacarpiennes") en comprend 4. Le nombre de ces épines métacarpiennes varie suivant les espèces et a de ce fait un intérêt diagnostique. Dans le cas présent, *L. wildi* se situe, parmi les petits *Leptodactylodon*, entre *L. bueanus*, à 3 épines, et *L. polyacanthus*, qui en possède 5 ou, presque aussi souvent, 6.

(2) Hypertrophie brachiale. Chez de nombreuses espèces de *Leptodactylodon*, les mâles se distinguent par l'hypertrophie de leurs bras et de leurs avant-bras. C'est le cas aussi chez *L. wildi*, où ce caractère est bien marqué, avec formation d'un "faux coude", dû à la saillie d'une des crêtes aliformes de l'humérus (voir à ce sujet AMIET, 1980).

En revanche, *L. wildi* ne présente pas de protubérances axillaires (excroissances dures situées à la racine des bras et produites par une apophyse basale de l'humérus). Ce caractère négatif est cohérent avec ce qu'avaient déjà montré les autres espèces de *Leptodactylodon* : les protubérances axillaires manquent chez celles dont les dents vomériennes sont bien développées.

(3) Spinosité cutanée. Alors que les caractères précédents rapprochent *L. wildi* de *L. polyacanthus*, l'aspect de la spinosité cutanée l'en sépare nettement. Contrairement à ce dernier, il n'y a pas de productions fortement kératinisées mais seulement d'infimes spinules incolores imperceptibles à l'œil nu. Ces productions tégumentaires se trouvent sur le pourtour des mâchoires supérieure et inférieure, de part et d'autre de l'anus, sur les talons, sur la face inféro-externe des tarses et sur la plante des pieds. La gorge et la région pectorale, fortement spinescentes chez diverses espèces et en particulier chez *L. polyacanthus*, sont totalement lisses chez *L. wildi*.

Cavité buccale. Le développement et la disposition des dents vomériennes fournissent chez les *Leptodactylodon* (contrairement aux autres Astylosterninae) de bons caractères taxonomiques (AMIET, 1980). Ici, elles constituent deux bandelettes subrectilignes largement séparées et plus courtes que chez les *Leptodactylodon* du groupe d'*ovatus*, leur extrémité externe atteignant à peine le niveau des choanes (fig. 4c). Cette extension est similaire à celle de *L. albiventris* et *L. polyacanthus*.

La langue, cordiforme, est étroitement et profondément échancrée à son extrémité ; elle ne présente ni papille ni fossette sur sa face supérieure.

Vocalisations. Les appels les plus souvent entendus sont des "toing" ou "toeng" espacés de quelques secondes, qui ressemblent curieusement aux sons produits par le relâchement d'une corde de guitare. Ils durent de 0,2 à 0,45 s et se présentent comme une série d'éléments serrés dont la fréquence est légèrement relevée vers la fin (fig. 5). La première harmonique est plus sonore que la fréquence de base (vers 2000 Hz) ; les harmoniques supérieures sont très faibles. L'enregistrement réalisé le 30 mars 1998 ne comprend pas d'autre type de cri et FDL n'a rien entendu d'autre sur la période du 30 mars au 3 avril. En décembre 1998, par contre, les appels de type corde pincée étaient fréquemment suivis d'un ou deux "krier" plus courts (fig. 5). Chez deux individus voisins dialoguant pendant plusieurs minutes, chacun émettait un "toing" suivi d'un ou deux "krier" (avec un intervalle entre les notes d'environ une seconde),

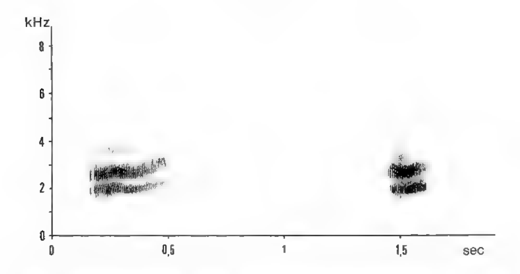


Fig. 5 – *Leptodactylodon wildi* appel à timbre de corde pincée "toeng" suivi de l'appel plus court "krier" Sonagramme produit en bande large sur un spectrographe Key Electric Co. de type 7029A (enregistrement et sonagramme F. Dowsett-Lemaire).

l'intervalle de réponse d'un individu à son voisin variait de une a quatre secondes. Les "krier" sont nettement plus courts, de l'ordre de 0,15 s et n'ont pas le timbre de corde pincée malgré la similitude des fréquences ; les unités sont en revanche plus serrées que dans l'autre type d'appel.

Le son de corde pincée est unique dans le genre *Leptodactylodon*, et même, de façon plus générale, parmi les anoures camerounais (environ 160 espèces enregistrées par JLA). L'autre cri, plus comprimé et plus "sec", est d'un type plus banal chez les *Leptodactylodon* et rappelle un peu, entre autres, celui de *L. perreti* (Amiet, 1980).

Distribution, écologie. En 1998, l'espèce a été repérée en deux points situés tous deux à 1350 m d'altitude et à proximité du village de Kodmin ("Kumin" sur la feuille Buea-Douala au 1/200.000; 9°42'E, 4°59'N), dans les monts Bakossi (fig. 6). Cet ensemble montagneux, relativement peu elevé (il culmine à 1895 m) mais très accidenté, double à l'ouest l'axe orographique majeur de la Dorsale camerounaise, constitué ici par l'alignement des monts Koupé, Manengouba, Ekomane, etc.

Dans ce secteur, entre les monts Bakossi et le mont Manengouba tout proche, l'altitude reste supérieure à 1200 m. Cela signifie que les deux massifs communiquent par un "pont" d'étage submontagnard (sensu Letouzey, 1985), situation qui autorise le passage, dans un sens ou dans l'autre, de nombreuses espèces orophiles, à l'exception de celles, inféodées à l'étage montagnard, qui restent isolées sur les parties culminales du Manengouba.

Le premier site où la présence de *L. wildi* a été constatée est à moins d'un kilomètre du village de Kodmin. Sa végétation correspond à une forêt basse croissant dans un petit ravin humide, avec de nombreuses fougères arborescentes (*Cyathea manniana* Hook) et de jeunes

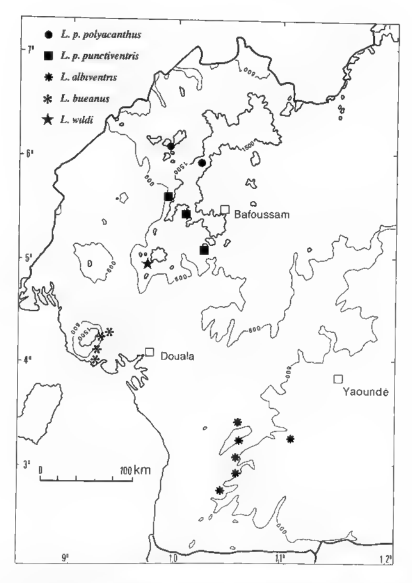


Fig. 6. – Carte de la partie sud-ouest du Cameroun, montrant la répartition des petits *Leptodactylodon* à dents vomériennes développées.

palmiers (*Phoenix reclinata* Jacq.). L'eau affleure par endroits, et un minuscule ruisseau coule en fin de saison des pluies. Dans ce secteur, les espèces compagnes suivantes ont été enregistrées par FDL et identifiées auditivement par JLA : *Phrynodon* sp. 2 (sensu AMIET, 1975), chantant exactement au même endroit, et, un peu plus bas, *Phrynobatrachus cricogaster* Perret, 1957, *P. werneri* (Nieden, 1910), *Phrynodon* sp. 1 (sensu AMIET, 1975), *Leptodactylodon mertensi* Perret, 1959 (?) et *Leptopelis brevirostris* (Werner, 1898).

Le second site est à environ 1,5 km de Kodmin, en forêt plus fermée (*Schefflera abyssinica* (Hochst. ex A. Rich.) Harms, *Polyscias fulva* (Hiern) Harms, *Cyathea manniana*), sur le versant ombragé d'un petit ruisseau. Les espèces compagnes sont ici *Phrynodon* sp. 1 et sp. 2, *Leptodactylodon mertensi* (?), *Cardioglossa melanogaster* Amiet, 1972, *Leptopelis brevirostris*, *L. calcaratus* (Boulenger, 1906) et *Afrixalus lacteus* Perret, 1976 (même mode d'identification que ci-dessus).

En mars 2000, de petites colonies ont été localisées par FDL en quatre endroits dans la forêt primaire au sud-ouest du village d'Edib (4°57'N, 9°39'E), à des altitudes comprises entre 1000 et 1200 m. Le milieu consistait toujours en zones marécageuses ombragées, un peu à l'écart des lits de ruisseaux, et à chaque endroit l'espèce co-existait avec *Phrynodon* sp. 2.

Les mâles de *L. wildi* chantent au sol, cachés dans des anfractuosités, sous les mousses ou les racines. Au site où l'espèce a été enregistrée, il y avait au moins une vingtaine de chanteurs dans un rayon de 10 m. Ils sont actifs à toute heure de la journée, mais davantage par temps couvert, et peuvent également chanter la nuit, jusqu'à deux heures au moins après le coucher du soleil.

Affinités. – Plusieurs espèces de *Leptodactylodon* sont caractérisées, comme *L. wildi*, par une petite taille (inférieure à 30 mm), des dents vomériennes bien développées disposées en crêtes transverses et une pigmentation terne et peu contrastée de la face ventrale. Il s'agit de *L. albiventris*, *L. bueanus* (décrit initialement comme sous-espèce de *L. albiventris* mais qui paraît en réalité spécifiquement distinct de ce dernier) et *L. polyacanthus*.

Les deux premiers ne sont pas orophiles mais sont localisés dans des régions accidentées qui reçoivent d'abondantes précipitations, alors que *L. polyacanthus* est un orobionte qui a une large répartition horizontale et verticale sur la Dorsale camerounaise. Ces trois espèces pourraient représenter un ensemble monophylétique un peu comparable à celui que constituent, par exemple, *Astylosternus batesi* (Boulenger, 1900), *A. diadematus* Werner, 1898 et *A. montanus* Amiet, 1977 (AMIET, 1977).

L. blanci, récemment décrit du Gabon sur un spécimen mâle (OHLER, 1999), peut être rapproché de ces derniers par sa petite taille et ses crêtes vomériennes bien développées mais s'en distingue par sa livrée ventrale vermiculée, patron qui n'était auparavant connu que chez les "grands" *Leptodactylodon* ; ses vocalisations sont inconnues, mais sa localité d'origine et la liste des quelques espèces capturées dans le même site montrent qu'il s'agit d'une espèce planitiaire.

Il est tentant de considérer *L. wildi* comme un vicariant géographique de *L. polyacanthus*, qui paraît manquer dans la partie sud du noyau principal de la Dorsale camerounaise (son absence sur le Mont Manengouba est signalée par AMIET, 1980). L'absence de spinosité corporelle kératinisée chez *L. wildi* constitue cependant un caractère différentiel important par rapport à *L. polyacanthus*, d'autant plus que ce type de caractère sexuel secondaire a

généralement tendance à s'exacerber chez les anoures orophiles. Cette absence est encore plus frappante quand on constate que *L. wildi* est, de tous les *Leptodactylodon* actuellement connus, la seule espèce à membres antérieurs hypertrophiés qui soit dépourvue de protubérances axillaires ou de spinosité gulaire et/ou pectorale. L'habitus de *L. wildi*, avec sa tête assez etroite et ses membres postérieurs très épais, le distingue aussi des autres petits *Leptodactylodon* à dents vomériennes développées.

Dans l'état actuel des connaissances, *L. wildi* peut être rapproche de ces derniers dans une clé de détermination (voir ci-après) mais cela n'implique pas qu'il leur soit étroitement apparenté. L'hypothèse qu'il représente à lui seul un petit phylum distinct ne doit pas être écartée. Elle pourrait être corroborée par la qualité acoustique extraordinaire des vocalisations qui ont conduit à sa découverte.

CLÉ D'IDENTIFICATION DES PETITS *LEPTODACTYLODON* À DENTS VOMÉRIENNES DÉVELOPPÉES

La clé d'identification suivante reprend une partie de celle de AMIET (1980), completee par OHLER (1999).

1. Mâles à bras non hypertrophiés, seulement un peu plus épais que ceux des femelles. Sac vocal développé, sa presence marquée par des plis paramandibulaires. Dessous (sauf la gorge) non maculé ou fortement vermiculé 2
1'. Mâles à bras hypertrophiés, sans plis paramandibulaires. Dessous plus ou moins maculé, mais les taches mal circonscrites, diffuses, en faible contraste avec le fond 4

2. Face ventrale foncee avec des vermiculations claires très apparentes. Taille du seul mâle connu : 22 mm. Trois épines métacarpiennes .... *L. blanci*
2'. Face ventrale, sauf la gorge, non maculée, rose saumon in vivo. Taille moyenne des mâles : 26 mm. Deux ou trois épines metacarpiennes 3

3. Doigts et orteils munis a leur extrémité de fins prolongements souples. Face dorsale d'un brun noirâtre uniforme a l'exception d'une barre interoculaire plus claire. Métacarpe des mâles avec 2 épines .... *L. albiventris*
3'. Doigts et orteils sans prolongements souples. Face dorsale bicolore, la partie postérieure du dos, la base des cuisses, etc., plus claires que le reste. Métacarpe des mâles avec 3 épines .... *L. bueanus*

4. Tête relativement etroite (T/L de l'ordre de 35 %). Taille plus faible : 21,5 a 23 mm chez les mâles. Face dorsale d'un brun clair olivâtre. Metacarpe avec 4 ou 5 epines chez les mâles, qui sont dépourvus de spinosité pectorale .... *L. wildi*
4'. Tête plus large (T/L de l'ordre de 39 %). Taille plus grande, 24,5 a 26 mm chez les mâles. Dessus d'un brun presque noir piquete de points bleutés. Metacarpe avec 5 ou 6 épines chez les mâles, qui sont pourvus de fortes épines pectorales noires réparties en deux plages triangulaires .... *L. polyacanthus*: 5

5. Triangles d'epines pectorales larges mais ne se rejoignant pas sur le milieu de la poitrine. Face ventrale plus ou moins assombrie mais depourvue de points ronds eclaircis .... *L. p. polyacanthus*

5' Triangles d'épines pectorales étroits, se rejoignant sur le milieu de la poitrine. Face ventrale ponctuée de clair sur fond sombre, au moins dans la région gulaire ... *L. p. punctiventris*

Résumé

Un nouveau *Leptodactylodon* orophile du Cameroun, *L. wildi*, est décrit à partir de spécimens trouves dans les Monts Bakossi (Cameroun). Cette espèce fait partie des petits *Leptodactylodon* à dents vomériennes bien développées, mais se distingue des taxons déjà connus par divers caractères morphologiques (taille plus faible, tête étroite, mâles dépourvus de spinosité cutanée et de plis gulaires mais à membres antérieurs hypertrophiés) et par ses appels très différents de ceux des autres *Leptodactylodon*, comparables au son produit par le relâchement d'une corde de guitare.

Remerciements

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Systematics of *Fejervarya limnocharis* (Gravenhorst, 1829) (Amphibia, Anura, Ranidae) and related species. 1. Nomenclatural status and type-specimens of the nominal species *Rana limnocharis* Gravenhorst, 1829

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A detailed analysis shows that the nominal species *Rana limnocharis* was first made nomenclaturally available by Gravenhorst (1829), and then a second time and independently by Wiegmann (1834). The consequences of these facts regarding the name-bearing types of these two nominal taxa are discussed and neotypes are designated for both of them. The status of the following related nominal species are also discussed, and their type-specimens are described: *Rana cancrivora* Gravenhorst, 1829; *Rana vittigera* Wiegmann, 1834; *Rana gracilis* Wiegmann, 1834; *Rana multistriata* Hallowell, 1861; *Rana wasl* Annandale, 1917. Finally, on the basis of several recent pieces of information, it is suggested that the group of frogs usually known as "*Rana limnocharis* group" or "subgenus *Fejervarya*" should be recognized as a distinct genus, *Fejervarya* Bolkay, 1915.

Abbreviations

Measurements

SVL Snout-vent length

Head

HW Head width.
HL Head length (from back of mandible to tip of snout).
MN Distance from back of mandible to nostril.
MFE Distance from back of mandible to front of eye.
MBE Distance from back of mandible to back of eye.

IFE Distance between front of eyes.
IBE Distance between back of eyes.
IN Internarial space.
EN Distance from front of eye to nostril.
EL Eye length.
SL Distance from front of eye to tip of snout.
NS Distance from nostril to tip of snout.
IUE Minimum distance between upper eyelids.
UEW Maximum width of upper eyelid.

Forearm

HAL Hand length (from base of outer palmar tubercle to tip of third finger)
FLL Forelimb length (from elbow to base of outer palmar tubercle)

Hindlimb

TL Tibia length
TW Maximum tibia width.
FOL Foot length (from base of inner metatarsal tubercle to tip of fourth toe).
TFOL Length of tarsus and foot (from base of tarsus to tip of fourth toe).
FL Femur length (from vent to knee).
MTTF Distance from distal edge of metatarsal tubercle to maximum incurvation of web between third and fourth toe.
TFTF Distance from maximum incurvation of web between third and fourth toe to tip of fourth toe.
MTFF Distance from distal edge of metatarsal tubercle to maximum incurvation of web between fourth and fifth toe.
FFTF Distance from maximum incurvation of web between fourth and fifth toe to tip of fourth toe.
IMT Length of inner metatarsal tubercle.
ITL Inner toe length

Museums and persons

AD Alain Dubois.
AMO Annemarie Ohler.
FMNH Field Museum of Natural History, Chicago, Illinois, USA.
MNHN Muséum National d'Histoire Naturelle, Paris, France
NMW Naturhistorisches Museum, Wien, Austria.
RMNH Nationaal Natuurhistorisch Museum, Leiden, Netherlands.
ZMB Zoologisches Museum, Berlin, Germany.
ZSI Zoological Survey of India, Calcutta, India.

INTRODUCTION

In most publications dealing with amphibians of south and south-eastern Asia, mention is made of very common small frogs that occur in or around most paddy fields, small ponds and open aquatic habitats of this region, and which are usually known under the name *Rana limnocharis*. Following BOULENGER's (1920*a*) work, this group was long viewed as a single species with four subspecies and this species was credited with a very wide distribution, from Pakistan to China and Japan and to Indonesia. However, on the basis of the study of mating calls and morphology, DUBOIS (1975*b*) showed that, in a very limited region (the small country of Nepal), no less than four distinct species did occur and had been confused under the name *Rana limnocharis limnocharis*. This author later showed that still other species were present in southern India (DUBOIS, 1984*b*) and suggested that the whole group was composed of at least 15 species, probably many more (DUBOIS, 1987, 1992). He further proposed (DUBOIS, 1984*b*, 1987, 1992) to remove this group from the genus *Rana* as understood by BOULENGER (1918, 1920*a-b*) and to recognize it provisionally as the subgenus *Fejervarya* Bolkay, 1915 of the genus *Limnonectes* Fitzinger, 1843. FEI et al. (1991) and YE et al. (1993) elevated this group to the rank of genus, but incorrectly under the generic name *Euphlyctis* Fitzinger, 1843 (a name which in fact applies to another group of species from the Indian region, that are much more aquatic than *Fejervarya* and that retain a lateral-line system in adults: see DUBOIS, 1992). Finally, DUBOIS (2000), ISKANDAR (1998, 1999), FEI (1999) and MARMAYOU et al. (2000) considered *Fejervarya* a distinct genus.

Within this frame, a question arises: to which species does the specific name *Rana limnocharis* apply? DUBOIS (1984*b*) suggested that it applies to populations of Java (from where the species was first described) and possibly of other regions, but that more work was necessary to establish the range of the "true" *Rana limnocharis*. The electrophoretic and morphometric data of TODA et al. (1998) and of VEITH et al. (2000) complicate this situation, as they show that two different species of this group live in Java. Which one should bear the name *Rana limnocharis*? Answering this question requires the clarification of the nomenclatural status and authorship of the name *Rana limnocharis*, to establish whether type-specimens of this nominal species can be identified and studied, and, if the answer to the last question is negative, to designate and describe a neotype for this taxon.

THE QUESTIONS

A great confusion exists in the literature regarding the nomenclatural status and author of the name *Rana limnocharis*. This name has been credited so far with seven different authorships: (1) "Kuhl" (without reference to a published text); (2) "Boie" (without reference to a published text); (3) WIEGMANN (1834, often miscited as "1835": see ZHAO & ADLER, 1993: 411-412); (4) Boie in WIEGMANN (1834); (5) Kuhl in GRAVENHORST (1829); (6) GRAVENHORST (1829); (7) Boie in GRAVENHORST (1829).

(1) The name *Rana limnocharis* first appeared in GRAVENHORST (1829: 42), who credited it to "Kuhl" and stated that this was a manuscript name appearing in an unpublished manuscript by Boie, where a closely related species was also described under the name *Rana cancrivora*.

(2) Shortly after, several authors (WAGLER, 1830: 203; TSCHUDI, 1838: 79; DUMÉRIL & BIBRON, 1841: 376, 379) mentioned the name *Rana limnocharis* as a label name credited to "Boie" that they had seen in the Leiden Museum. WIEGMANN (1834: 255-258; 1835: 277-278) compared his new species *Rana vittigera* and *Rana gracilis* to "*Rana limnocharis* H. Boje" or "*Rana limnocharis* Boie", a name for which he did not provide a reference. Then this name was forgotten for over 20 years, and the name *Rana gracilis* Wiegmann, 1834 was used for the species it denotes, until the name *Rana limnocharis* was resurrected by PETERS (1863: 77-78; 1871: 647), who cited WIEGMANN's (1834) text, credited the name to "Boie in Leyd[en] Museum", and stated that it should replace the name *Rana gracilis*. This was followed by STOLICZKA (1872: 102; 1873: 112), who however introduced the incorrect subsequent spelling *Rana lymnocharis* and credited it to "Boie", still without a reference.

(3) After having used the name *Rana gracilis* (BOULENGER, 1882: 28), BOULENGER (1890: 450) resurrected the original spelling *Rana limnocharis* and credited authorship of this name to WIEGMANN (1834). This interpretation was followed, among others, by STEJNEGER (1907: 127; 1910: 95), BARBOUR (1912: 64), BOULENGER (1912: 236), SMITH (1916: 165), ANNANDALE (1917: 132), KIRTISINGHE (1957: 38), NAKAMURA & UÉNO (1963: 49) and GORHAM (1974: 146).

(4) BOULENGER (1920*a*: 28) presented a slightly different interpretation, since he credited the species's name to Boie in WIEGMANN (1834). This was accepted by many authors, including VAN KAMPEN (1923: 167), LIU (1950: 315), INGER (1954: 267-268; 1966: 205), LIU & HU (1961: 139), BERRY (1975: 73), ANONYMOUS (1977: 81), FROST (1985: 500), MAEDA & MATSUI (1989: 108), FEI et al. (1991: 302), YANG (1991: 131), YE et al. (1993: 249), ZHAO & ADLER (1993: 144) and DUTTA & MANAMENDRA-ARACHCHI (1996: 91).

(5) STEJNEGER (1925: 27) was the first to point out that the name *Rana limnocharis* had first been published by GRAVENHORST (1829), and that the latter had credited this name to Kuhl. In the synonymy of this species, he therefore wrote its full original name as follows: "*Rana limnocharis* 'Kuhl' Gravenhorst". This writing was also used by FANG & CHANG (1931: 111).

(6) However, many subsequent authors only mentioned GRAVENHORST (1829) as author of the name, without mentioning Kuhl's "original authorship": this was the case, among others, of GEE & BORING (1929: 30), POPE (1931: 491), BORING et al. (1932: 35), CHANG & HSU (1932: 174), BORING (1934: 20; 1945: 82), POPE & BORING (1940: 50), BOURRET (1942: 249), TAYLOR & ELBEL (1958: 1051), TAYLOR (1962: 380), OKADA (1966: 112), DUBOIS (1984*b*: 143; 1992: 315), CHOU & LIN (1997: 27), DUTTA (1997: 133), MANTHEY & GROSSMANN (1997: 97) and FEI (1999: 182).

(7) Finally, DUBOIS (1974: 382-383; 1981: 238) cited this name as "*Rana limnocharis* Boie in GRAVENHORST, 1829".

Despite this great diversity of interpretations, few discussions were clearly devoted to the correct authorship of the name.

INGER (1954: 267-268) stated that the first "adequate description" of *Rana limnocharis* was to be found in WIEGMANN's (1834) text, where the name was credited to Heinrich Boie. INGER (1954) reported having seen a copy of the unpublished manuscript of Boie's original description of *Rana limnocharis*, and he concluded that the name *Rana limnocharis* should be credited to Boie in WIEGMANN (1834).

DUBOIS (1974: 382-383) noted that the first published mention of the name *Rana limnocharis* was in GRAVENHORST (1829), but that this latter author, although not very explicitly, credited it to Boie: he therefore suggested to cite this name as "*Rana limnocharis* Boie in GRAVENHORST, 1829". Subsequently however (DUBOIS, 1984*b*), he realized that GRAVENHORST (1829) was responsible both for first publication of the name and for satisfying the criteria of its availability, and was therefore its sole author, in the technical nomenclatural sense of this term. However, he did not provide a detailed explanation of these reasons to reject INGER's (1954) interpretation.

ZHAO & ADLER (1993: 144) concurred with INGER (1954), and provided several reasons for refusing to credit GRAVENHORST (1829) with the authorship of the valid name of this species: "The name was introduced in Gravenhorst's synonymy of *R. cancrivora*, not as a proper species name, but as a description of frogs living in small pools (hence his use of the word '*Ranae*' rather than *Rana*). Furthermore, we regard Gravenhorst's short description as unidentifiable. Boie's name, accompanied by a full description and a figure, is the first clear association of the name *R. limnocharis* with this taxon." In their synonymy of *Rana limnocharis*, these authors listed two distinct nominal species, each one with its own author and date: first "*Ranae limnocharis* Gravenhorst, 1829" and second "*Rana limnocharis* Boie in WIEGMANN, 1834". According to these authors, only the first of these two nominal species has a clear type locality (Java), while for the second one they wrote: "Type locality: none given". Finally, they stated that the first name was a "nomen dubium" and they wrote the valid name of this species as follows: "*Rana limnocharis* Boie, 1834".

These discussions may appear exaggeratedly quibbling, if not gratuitous, but they are not: according to the interpretation chosen, the nominal species *Rana limnocharis* may have four different authors and two different dates, and more importantly, it may be based on four different name-bearing types. If Kuhl is retained as author of the name, the type-specimens of the nominal species will be the specimens collected by Kuhl & Van Hasselt, and distributed later in several museums; if Boie is the author, only those specimens kept in Leiden when he prepared his description and figure will be types; if Gravenhorst is the author, the name-bearing type will be the specimens examined by this author in Breslau; finally, if Wiegmann is the author, it will be the specimens examined by this author in Berlin. According to the interpretation chosen, different specimens will have to be considered types, and in some cases all types will be lost; this will have consequences regarding the possible choice of a lectotype or neotype for the nominal species *Rana limnocharis* and the allocation of this name to one of the two biological species occurring in Java. A detailed analysis of the history of the case and of the various problems pointed out above regarding the availability of names is therefore in order before any such designation of lectotype or neotype. To avoid criticism, this discussion must be made strictly within the frame of the current *International Code of Zoological Nomenclature* (ANONYMOUS, 1999, cited below as "the *Code*"), which means that some technical nomenclatural terms and rules will have to be mentioned below.

Nomenclatural status and authorship of the name *Rana limnocharis*

Historical survey of the discovery, collecting and naming of *Rana limnocharis*

The first documented discovery and collection of *Rana limnocharis* was by H. Kuhl & J. C. Van Hasselt, during their brief stay in Java (respectively 1820-1821 and 18[illegible]-1823) which ended with the death of both of them (see e.g.: Brongersma, 1942; Adler, [illegible]). These two naturalists collected several specimens of a small species of frogs common around paddy fields, for which they apparently coined the name *Rana limnocharis*. However, unlike for other amphibian species (see e.g. Dubois, 1982), this name was not mentioned in the copies of the letters sent by them to Europe that were published in three different zoological journals (Kuhl & Van Hasselt, 1822*a-b*; Van Hasselt, 1823; Kuhl, 1824*a-b*). They sent specimens of this species to the Rijksmuseum van Natuurlijke Historie (now the Nationaal Naturhistorisch Museum) in Leiden, where these were apparently labelled under two different names, "*Rana cancrivora*" for the large ones and "*Rana limnocharis*" for the small ones. Apparently, in this collection the second of these names was credited to Kuhl, as is implied by the mention of "*Ranae limnocharis* Kuhlii" in Gravenhorst (1829: 42), while the name *Rana cancrivora* seems to have been coined by Heinrich Boie, in the manuscript of his *Erpétologie de Java*: this latter book, announced by Schlegel (1826, 1827) and Gravenhorst (1829), was never published, although it had been sent to the printer in 1830 (see Brongersma, 1942). The fact that specimens labelled under the two above names were kept in the Leiden Museum was reported by Wagler (1830: 203) and Tschudi (1838: 39, 79). Furthermore, according to Schlegel (1827: 282) and Duméril & Bibron (1841: 379), some other specimens of this group collected by Kuhl & Van Hasselt were also sent to other European Museums: this is precisely documented at least in two cases, for two specimens in the Breslau (now Wroclaw) Museum mentioned by Gravenhorst (1829: 41-42) and for two specimens in the Berlin Museum mentioned by Wiegmann (1834: 57-58).

The first publication of the name *Rana limnocharis* was by Gravenhorst (1829: 42). This name was only briefly mentioned in the chapter dealing with a species described as new under the name *Rana cancrivora*, where, after a Latin diagnosis of the latter species, one can read: "Hujus speciei Javanensis de Haan duo individua mecum communicavit, unum, idque majus, capite vix paulo obtusiore, corporis totius facie infera fusco- et fusco-ferrugineo-maculata, sub nomine *Ranae cancrivorae*, minus, idque facie infera corporis albida immaculata, sub nomine *Ranae limnocharis* Kuhlii. Conferantur quae ad *Hylam leucomystacem*, n. 4, monui." (Gravenhorst, 1829: 41-42). Above in the same volume, the following appears under *Hyla leucomystax*: "Cum de Haan, conservator humanissimus musei Lugdunensis, hanc *Hylam leucomystacem* Kuhlii javanensem, pluresque alias species, Javae indigenas, ad me transmitteret, simul me certiorem faciebat, Boieam descriptiones et icones reptilium novorum Javanensium, in peculiari *Erpetologia*, editurum esse. Inde harum specierum solas diagnoses circumscriptas proferam, ne auctori *Erpetologiae* temere antevertam. Utinam opus exoptatissimum mox in lucem proderat! Conferas conspectum hujus *Erpetologiae*, quem Schlegel in *Bulletin des Sci. nat.* 1826, n. 10, pag. 233-240 edidit." (Gravenhorst, 1829: 26)

These statements can be summarized as follows: (1) de Haan, Curator at the Leiden Museum, had sent specimens, including several of the new frog species collected in Java by Kuhl & Van Hasselt, to the Breslau Museum; (2) while doing so, he had informed Gravenhorst in Breslau that, in a book already written but not yet published (and summarized by SCHLEGEL, 1826), Boie had provided descriptions and figures of several new herpetological species from Java; (3) in the expectation of the publication of this book, Gravenhorst decided to publish only short diagnoses of the new Javanese species he had received from de Haan, (4) among those were two frog specimens, a large one under the name *Rana cancrivora* and a smaller one under the name *Rana limnocharis*; (5) Gravenhorst's opinion was that these two specimens, which also differed by the shape of the snout and the colour of the lower parts of the body, belonged to a single species, for which he chose the name *Rana cancrivora* and provided a Latin diagnosis.

As mentioned above, ZHAO & ADLER (1993) considered the status of the name *Rana limnocharis* in GRAVENHORST (1829) as questionable, and decided not to apply this name to the species. Let us consider their arguments.

AN ANALYSIS OF ZHAO & ADLER'S (1993) STATEMENTS

Several distinct reasons for not recognizing GRAVENHORST (1829) as the author of the name *Rana limnocharis* can be sorted from ZHAO & ADLER's (1993) short statements (see above). Let us distinguish them and clearly formulate them in precise technical nomenclatural terms.

(1) ZHAO & ADLER (1993) first stated that the name *Rana limnocharis* "was introduced in Gravenhorst's synonymy of *R. cancrivora*". Although they did not discuss this point further, this statement can be understood as meaning that the name *Rana limnocharis* was not made nomenclaturally available in GRAVENHORST's (1829) work for the mere reason that it had been introduced there as a synonym.

(2) The next statement of ZHAO & ADLER (1993) is that the name *Rana limnocharis* was proposed "not as a proper species name, but as a description of frogs living in small pools". Strictly taken, this statement does not mean much, since, of course, a new species name can well be proposed for frogs living in small pools. What ZHAO & ADLER (1993) apparently meant was that the two words *Rana limnocharis* were not proposed as the name of a new species-group taxon, but merely as a statement aiming at giving some biological characterisation of a frog species, which otherwise was remaining unnamed. In nomenclatural terms, this means that in GRAVENHORST (1829) the combination *Rana limnocharis* was a kind of "formula" without nomenclatural status, i.e. that the name *Rana limnocharis* was nomenclaturally *unavailable* in this text.

(3) In support of this interpretation, ZHAO & ADLER (1993) claimed that the use of the word "*Ranae*" instead of *Rana* shows that GRAVENHORST (1829) was referring to "frogs" rather than to a frog species. In other words, and to put this in grammatical and nomenclatural terms, they apparently believed that "*Ranae limnocharis*" was a nominative plural, and therefore, for this mere reason, nomenclaturally *unavailable* under the *Code* for the name of a new species-group taxon. Although they did not state this in full words, it seems that what

Zhao & Adler (1993) had in mind is the fact that Article 11.9.1.1 of the *Code* requires that, to be available, a new species-group name should be in the nominative singular

(4) Statements (1) to (3) tend to show that Zhao & Adler (1993) regarded the name *Rana limnocharis* as nomenclaturally *unavailable*. However, in their next sentence, as well as in the synonymy of the species, they adopted another interpretation, since they insisted on the fact that the short description of *Rana limnocharis* in Gravenhorst (1829) was "unidentifiable" and that this name was therefore a "nomen dubium". This interpretation is quite different from, and actually contradictory to the previous one. according to the *Code* (Anonymous, 1999: 111), a "nomen dubium" is a "name of unknown or doubtful application", i.e. a name nomenclaturally *available* but whose *allocation* to a biological taxon is impossible or doubtful. For this reason, Recommendation 75.E of the 1985 edition of the *Code* (Anonymous, 1985: 163) aptly suggested to designate neotypes for species-group nominal taxa "to clarify the application of names when their continued existence as nomina dubia threatens the stability of other names", a formulation that has unfortunately disappeared in the last edition of the *Code*.

To sum up, statements (1) to (3) of Zhao & Adler (1993) support the idea that the name *Rana limnocharis* is nomenclaturally *unavailable* in Gravenhorst's (1829) text, while their statement (4), as well as their inclusion of this name in their synonymy of the species, supports the opinion that this name is nomenclaturally *available* but of *doubtful allocation* to a biological species, and therefore cannot be used. An important weakness of this interpretation is its failure to address the following problem: if two distinct nominal species are to be recognized, the second name is a junior primary homonym of the first one and therefore an invalid name. In other words, if, as clearly implied by the end of their text, the name "*Rana limnocharis* Gravenhorst, 1829" was both (1) an available name and (2) inappropriate for the species, being a "nomen dubium", then the species would have to bear another name as the only other synonym, beside "*Rana limnocharis* Boie, 1834", listed by Zhao & Adler (1993), is *Rana gracilis* Wiegmann, 1834, which is also a primary homonym in the genus *Rana* (see e.g. Dubois, 1984*b*: 154), no name would be available for the species and a new name would have to be coined for it!

Is the name *Rana limnocharis* in Gravenhorst (1829) available under the *Code*?

Let us first consider the statements (1) to (3) of Zhao & Adler (1993). According to these statements, the name *Rana limnocharis* would be nomenclaturally unavailable in Gravenhorst's (1829) text for three distinct but complementary reasons: (1) this name was published there as a synonym; (2) this name would not have been proposed to designate a frog taxon, but merely to refer "informally" to a "kind" of frogs without "naming" them; (3) this name would appear in Gravenhorst's text as a nominative plural, not as a nominative singular as required by Article 11 of the *Code*.

(1) As correctly stated by Zhao & Adler (1993), the name *Rana limnocharis* was first published by Gravenhorst (1829) as a junior synonym of the name *Rana cancrivora*. What are the nomenclatural consequences of this fact? The *Code* is quite clear about the nomenclatural status of names first published as synonyms. Article 11.6 reads as follows: "A name [...] first published [...] as a junior synonym [...] is not thereby made available" unless it has been "treated before 1961 as an available name and either adopted as the name of a

taxon or treated as a senior homonym", such a name "dates from its first publication as a synonym". The name *Rana limnocharis* mentioned in GRAVENHORST (1829) clearly corresponds to this situation, since it has regularly been treated as an available name since STEJNEGER (1925): it therefore dates from its first publication as a junior synonym of *Rana cancrivora*.

(2) Close examination of the whole book of GRAVENHORST (1829) also allows to unambiguously reject interpretation (2). The name "*Ranae limnocharis*" is composed of two words, a generic name bearing a capital and a specific name starting with a lower-case letter, as are all other scientific names of species in the book. This name is printed with wide spaces between letters, which would correspond to italics in modern printing: in GRAVENHORST's book, such a way of printing is used only for scientific names of taxa and for some other words that the author wanted to stress as particularly important in his text. Finally, this name is followed by the mention "Kuhlii", i.e. a genitive meaning "of Kuhl", clearly indicating that in GRAVENHORST's mind Kuhl was the author of this name. The name "*Ranae limnocharis*" was thus clearly intended to designate a taxon. Nothing in this text gives the slightest support to the interpretation that this name would be a "formula" informally designating a "kind" of frogs.

(3) ZHAO & ADLER (1993) are also incorrect when they consider the name "*Ranae limnocharis*" to be a nominative plural meaning "frogs living in small pools". As was underlined by BOUR & DUBOIS (1984), the *Code*'s requirement that species-group names, to be nomenclaturally available, be published in the nominative singular, makes sense only when the whole text is written in a language other than Latin: in a Latin text, the grammatical case of words is determined by their place in the sentence, and only names occupying the place of subjects can be written in the nominative, in all other situations, the grammatical case of names will have to be different. We are here exactly in this situation: actually, considering the structure of GRAVENHORST's Latin sentence (quoted above), it is clear that the name "*Ranae limnocharis*" was in the genitive singular and meant "of *Rana limnocharis*". All the text of GRAVENHORST (1829) being written in Latin, in the sentence as it was written the use of the genitive singular was compulsory. This case corresponds to the situation described in Article 11 of the *Code*: "A genus-group name proposed in Latin text but written otherwise than in the nominative singular because of the requirements of Latin grammar is available, provided that it meets the other requirements of availability, but it is to be corrected to the nominative singular." (Article 11.8.1); "An adjectival species-group name proposed in Latin text but written otherwise than in the nominative singular because of the requirements of Latin grammar is available provided that it meets the other requirements of availability, but it is to be corrected to the nominative singular if necessary." (Article 11.9.2).

Reasons (1) to (3) given by ZHAO & ADLER (1993) to refuse nomenclatural availability of the name *Rana limnocharis* in GRAVENHORST (1829) are therefore to be rejected. Could there be other reasons to refuse this availability? In other words, does this name meet the "other requirements of availability" mentioned in the *Code*? The answer to this question is clearly "yes": all criteria mentioned in Articles 10, 11 and 12 of the *Code* are met with.

In conclusion of this section, the name *Rana limnocharis* as published in GRAVENHORST's (1829) text is clearly available in zoological nomenclature. Let us now see to which taxon this name applies.

Is the name *Rana limnocharis* in Gravenhorst (1829) a "nomen dubium"?

To be sure, the "description or definition" (in the sense of Article 12 of the *Code*) given to diagnose *Rana limnocharis* in Gravenhorst (1829) is very short and vague, and liable to cause problems for the *allocation* of this name to a biological taxon, although it does not pose a problem regarding the *nomenclatural availability* of the name. Dubois & Ohler (1995, 1997*a-b*) discussed the problems posed by old names based on incomplete or insufficient descriptions. They remarked that the nomenclatural allocation of a name to a taxon does not rely on its description, definition or diagnosis, but on its type-specimens, either actual or potential, and through these specimens to the type-population from which these had been collected. Actually, in frogs, many taxa named in the 18th and early 19th century were first provided with very short and fully insufficient diagnoses or descriptions, and the types have often been lost, but this has no bearing on the availability of names: in most of these cases, the status of these names was later fixed through redescriptions by the same or other authors, re-examination of holotypes or syntypes, or designation of neotypes. As short as it is, the statement that *Rana limnocharis* is smaller than *Rana cancrivora* and has a different snout shape and belly coloration is enough to make the former name nomenclaturally available, even if it is not enough to ascertain the taxonomic allocation of this name to a biological species. To solve the problem of the allocation of the name *Rana limnocharis* to a frog taxon, it is necessary to identify the name-bearing type of this taxon. As mentioned above, the status of this/these type-specimen(s) is directly linked to the authorship of this name. Before addressing this question however, let us consider more generally the rules governing authorship in zoological nomenclature according to the current *Code*.

Authorship of names "borrowed" from manuscripts or collection labels

Article 50.1 of the *Code* provides the following definition of "author" in zoological nomenclature: "The author of a name [...] is the person who first publishes it [...] in a way that satisfies the criteria of availability [...]. However, if it is clear from the contents [of the publication] that some person other than an author of the work is alone responsible both for the name [...] and for satisfying the criteria for availability other than actual publication, then that other person is the author of the name [...]". Particularly important, and often overlooked by taxonomists, are the terms "*alone* responsible". These statements mean that the author of a scientific name according to the *Code* is *not* any of the following: (1) the person(s) who actually *coined* the name, or the person(s) who wrote the first unpublished *description* or *definition* of the taxon, or provided any other information that could be an *indication* making the name available under the *Code*, unless in the first valid publication of the name it was made quite clear, in full words, that both the name and the published description, definition or indication were directly copied, without any modification (i.e., "verbatim"), from this unpublished document; (2) any person who could have *used* this name in conversations, meeting or unpublished documents, such as letters or labels attached to specimens in zoological collections.

According to such stringent rules, the case is much rarer indeed than is often believed by many zoologists where a situation qualifies for authorship of a name being validly stated to be

"XXX in ZZZ". This applies to cases where a name was first published by an author who stated clearly (1) that this name was provided to him/her privately by another colleague, but (2) that he/she personally had never seen specimens of the taxon. A good example of this situation is the European frog name *Rana dalmatina*, which was first validly published by BONAPARTE (1838) in a text where he stated that he had not seen this species, but that the latter had been mentioned to him, and briefly described, by Fitzinger in an unpublished letter: this species must therefore be known as *Rana dalmatina* Fitzinger in BONAPARTE, 1838 (see DUBOIS, 1984*a*). But this situation is rather rare indeed. In most cases, the author who first published a name had seen specimens of the taxon, and added (or may have added) some observations or statements of his/her own concerning the latter: in such cases, even if this author credited the new name to the person who had coined it, in the strict sense of the *Code* the author is the person who published it. Such a practice of publishing manuscript names credited to other authors was very common in the early 19th century. Several examples of this situation can be found e.g. in TSCHUDI's (1838) work. Tschudi "borrowed" a number of names from DUMÉRIL & BIBRON's (1841) then still unpublished book and from other manuscripts: although he duly credited these names to their "proper" authors such as Bibron or Schlegel, Tschudi had clearly examined personally specimens of these taxa, and used these observations to write their brief descriptions or diagnoses, so that he is no doubt the author, in the technical nomenclatural sense of the term, of these names.

A particular case must however be made for names first published as junior synonyms. Article 50.7 of the *Code* reads as follows: "If a scientific name (taken, for example, from a label or manuscript) was first published in the synonymy of an available name and became available before 1961 through the provisions of Article 11.6, its author is the person who published it as a synonym, even if some other originator is cited, and is not the person who subsequently adopted it as a valid name [...]." Therefore, in the case of a name first published as a junior synonym and a posteriori validated through use by subsequent authors, in all cases the author is the person who first published it, and in no case the writing "XXX in ZZZ" can be used.

WHO IS THE AUTHOR OF THE NAME *RANA LIMNOCHARIS* IN GRAVENHORST (1829)?

It was shown above that the name *Rana limnocharis* was nomenclaturally available from the publication of GRAVENHORST (1829). The question now remains: who is the author, in the technical sense of this term in the *Code*, of this name? Four possible authorships can be considered: GRAVENHORST (1829), Kuhl in GRAVENHORST (1829), Kuhl & Van Hasselt in GRAVENHORST (1829) and Boie in GRAVENHORST (1829).

While it is difficult at present to ascertain who really *coined* the name *Rana limnocharis*, GRAVENHORST (1829) provided two different pieces of information in this respect. (1) this name was attached to the label of one of the frog specimens sent by de Haan to the Breslau Museum, and it was stated to be one of the names of taxa described as new by Boie in his unpublished *Erpetologie de Java*. (2) however, by writing "Kuhlii" after this name, Gravenhorst clearly suggested that the name had been coined by Kuhl, not by Boie. The most likely explanation of this apparent contradiction is that Boie himself, in his manuscript description of the species, credited its name to Kuhl (or to Kuhl & Van Hasselt), possibly because this name was already present in Kuhl's labels or manuscript notes sent with the specimens from

Java. Whatever the case may be, this is of purely historical but of no nomenclatural importance. The name *Rana limnocharis* having been published in GRAVENHORST (1829) as a junior synonym and a posteriori validated by STEJNEGER (1925) and other subsequent authors, according to Article 50.7 the author of this name is clearly GRAVENHORST (1829), irrespective of who had coined it before its first publication.

THE STATUS OF THE NAME *RANA LIMNOCHARIS* BETWEEN 1829 AND 1863

After the book of GRAVENHORST (1829), the first published occurrence of the name *Rana limnocharis* was in WAGLER (1830: 230), who listed this species as valid among the species of the genus *Rana*. WAGLER (1830) did not refer however to GRAVENHORST's (1829) text, but to an unpublished label by Boie in the Leiden Museum, and he provided no description, diagnosis or indication characterising the species. It cannot therefore be argued that WAGLER (1830) referred to the name *Rana limnocharis* Gravenhorst, 1829, and the name *Rana limnocharis* in his text must be considered a nomen nudum, without status in nomenclature.

The situation is different in WIEGMANN's (1834) book, the second published text providing descriptive data on *Rana limnocharis*. WIEGMANN described two new species, *Rana vittigera* and *Rana gracilis*, both of which he compared with "*Rana limnocharis* Boie". He stated that the Berlin collection possessed two specimens of the latter species: most probably, although this is not stated in this text, these specimens were also part of those collected by Kuhl & Van Hasselt in Java and had been obtained from the Leiden Museum. Later in the same text, WIEGMANN (1834: 260) stated that he had received the new species "*Hyla quadrilineata* H. Boje in *Mus. Lugd.*" from Wagler (who was in München), thus clearly indicating the presence in the Berlin collection of specimens from Boie's material.

What is the status of the name *Rana limnocharis* in WIEGMANN (1834)? Although he credited the name to Boie, WIEGMANN (1834) did not cite the manuscript of the *Erpétologie de Java*, nor GRAVENHORST's (1829) book. The absence of any reference to the latter work in the whole text precludes considering WIEGMANN (1834) as having used the name *Rana limnocharis* Gravenhorst, 1829. Rather, this author used an unpublished label or manuscript name, which he made nomenclaturally available, independently from GRAVENHORST (1829), by publishing rather detailed descriptive data on this species. Therefore, WIEGMANN (1834) created a new, distinct, nominal species. Who is the author, in nomenclatural terms, of this name? The situation here is different from that discussed above for *Rana limnocharis* Gravenhorst, 1829, since in WIEGMANN's case the new name was not published as a junior synonym but as a valid name, credited to Boie. In this case, Article 50.1 of the *Code* applies, and despite WIEGMANN's himself crediting this name to Boie, there is no doubt that the author is WIEGMANN (1834), who described several precise morphological features of the species, clearly drawn from personal examination of the two specimens in his hands.

WIEGMANN (1835: 277-278) summarized his 1834 work and mentioned again the name *Rana limnocharis*. This name then appeared twice as a junior synonym in TSCHUDI (1838: 79) and in DUMÉRIL & BIBRON (1841: 376, 379), who referred to unpublished manuscripts or labels, and was then apparently ignored by all authors until PETERS (1863) resurrected it and

cited WIEGMANN's (1834) text. From 1863 this name was no longer used as a nomen nudum, but as a name considered validly published in WIEGMANN (1834), or, after STEJNEGER (1925), in GRAVENHORST (1829).

STATUS OF THE ORIGINAL NAME-BEARING TYPES

As mentioned above, identification of the proper author, in the precise nomenclatural sense of the term, of a scientific name, is crucial, as it implies identification of the proper name-bearing type of the nominal taxon, which ultimately allows proper allocation of the name to a biological taxon

The analysis above has shown that two distinct nominal species bearing the name *Rana limnocharis*, with different authors and dates, should be recognized: it results that both nominal species have their own name-bearing type, which must be identified

THE ORIGINAL NAME-BEARING TYPE OF *RANA LIMNOCHARIS* GRAVENHORST, 1829

The name *Rana limnocharis* Gravenhorst, 1829 was first published as a junior synonym and therefore falls under the provisions of Article 72 4 3 of the *Code* "The type series of a nominal species-group taxon of which the name was first published as a junior synonym, but was made available before 1961 under the provisions of Article 11 6, consists of the specimen (or specimens) cited with that name in the published synonymy, or, if none was cited there, denoted by that name when it was adopted as the name of a taxon".

The situation in GRAVENHORST (1829) is particularly clear, as this author stated in full words that he had received from de Haan a single specimen labelled *Rana limnocharis*. This specimen was therefore the holotype by monotypy of *Rana limnocharis* Gravenhorst, 1829 This specimen was kept in the Breslau (now Wroclaw) Museum, and apparently no information about it was published posterior to GRAVENHORST's (1829) book In reply to a request of 23 May 1997, on 6 June 1997 Prof Andrej Wiktor (Muzeum Przyrodnicze, Uniwersytet Wroclawski) informed one of us (AD) by letter that the only remaining specimens of the Gravenhorst collection are some insects, and that attempts to find specimens of other groups before the Second World War were unsuccessful

The holotype of *Rana limnocharis* Gravenhorst, 1829, collected in Java by Kuhl and Van Hasselt between 1820 and 1823, must therefore be considered lost, and definitive stabilization of the status of this name will require the designation of a neotype.

THE ORIGINAL NAME-BEARING TYPE OF *RANA LIMNOCHARIS* WIEGMANN, 1834

According to the analysis presented above, the name *Rana limnocharis* Wiegmann, 1834 was based on descriptive information published by WIEGMANN (1834) after examination of two specimens of "*Rana limnocharis* Boie" in the Berlin Museum, presumably collected by Kuhl and Van Hasselt in Java and received from the Leiden Museum These two specimens

were therefore the original syntypes of this nominal species. These two specimens are apparently lost: according to Rainer Gunther (e-mail to AMO of 30 November 1998), the Berlin Museum collection does not have a single specimen of *Rana limnocharis* collected by Kuhl or Kuhl and Van Hasselt in Java. Final stabilization of the status of this name also requires the designation of a neotype.

Specimens available for neotype designations

In order to definitely avoid possibilities of nomenclatural confusion, and to know which of the two "sibling" species in Java should bear the name *Rana limnocharis* Gravenhorst, 1829 (see Veith et al., 2000), designation of a neotype for this nominal species is necessary. As for the name *Rana limnocharis* Wiegmann, 1834, being a junior primary homonym it is an invalid name and its existence does not threaten the stability of nomenclature, but, in order to know in which synonymy it will have to stand, a neotype designation is also necessary. The most logical action is to place it in the synonymy of *Rana limnocharis* Gravenhorst, 1829. Since neotypes have to be designated for both nominal species, the most parsimonious solution is to choose the same specimen as neotype of both: these two names will then be linked by an objective synonymy and no further discussion of their status should arise in the future.

Which specimen would be best suited for this neotype designation? Both nominal species were created on the basis of specimens collected in Java by Kuhl and/or Van Hasselt and sent to the Breslau and Berlin Museums from the Leiden Museum. These specimens being lost, it seems appropriate to look for other specimens collected in Java by these naturalists and kept in the Leiden Museum or in other museums under the name *Rana limnocharis*, or possibly also of *Rana cancrivora* (as both species were considered synonyms by some ancient authors, including Gravenhorst, 1829). Both Schlegel (1827) and Dumeril & Bibron (1841) stated that such specimens had been sent to several other European museums, but unfortunately these authors did not specify which ones. Published and unpublished information was therefore gathered about this question, with the following results. (1) no specimens under these two specific names and collected in Java by Kuhl and/or Van Hasselt are to be found in the old collections of the museums of Basel (Muller, 1878, 1880, 1882, 1883, 1885, 1887, 1889, 1892, 1901), Frankfurt am Main (Boettger, 1892, Mertens, 1967, AD & AMO, personal observations), London (Nick Arnold, e-mail to AMO of 27 March 1998), München (Frank Glaw, e-mail to AD of 31 March 1998), Paris (AD & AMO, personal observations) and Wien (Heinz Grillitsch, e-mail to AD of 24 March 1998), (2) the Leiden Museum still has a single specimen of this group, RMNH 4287 (Marinus S. Hoogmoed, e mail to AD of 16 March 1998). This latter specimen, kept under the name *Rana limnocharis*, is stated to have been collected by Kuhl in Java (no information is available on locality and date of collection). It is a young female in rather good condition, and this specimen, described below, is fully appropriate for neotype designation, although unfortunately it has no precise locality. Given the information provided in the letters sent by Kuhl and Van Hasselt from Java, it seems likely that this specimen was collected in the vicinity of Buitenzorg, now Bogor: "En nog zijn wij geen 20 uren ver van Buitenzorg gekomen" ("And until now we did not go further than 20 hours from Buitenzorg") (Kuhl & Van Hasselt, 1822*a*: 103).

STATUS OF A FEW NAMES CLOSELY RELATED TO THE NAME *RANA LIMNOCHARIS*

As mentioned above, for a long time the name *Rana limnocharis* was applied indiscriminately to small frogs from a wide area of south and south-eastern Asia. As a number of different names had been proposed in the beginning of zoology for frogs of this complex, these names were long considered either to be synonyms of *Rana limnocharis* or, at best, to apply to subspecies of the latter species. During the second half of our century, in this group and many others (see DUBOIS & OHLER, 1998), the strong "lumper philosophy" of INGER (1954, 1966) had a drastic influence on the taxonomy adopted by most authors: thus, INGER (1954: 267-274, 1966: 205-206) treated the taxon *Rana vittigera* Wiegmann, 1834 from the Philippines as a subspecies of *Rana limnocharis*, as for the name *Rana wasl* Annandale, 1917, although this name clearly applied to frogs of this complex and was based on a type-specimen from Borneo, he ignored it altogether in his book on Bornean frogs (INGER, 1966). DUBOIS (1975*b*, 1984*b*, 1987, 1992) showed that this complex was in fact composed of a number of distinct species, and gave a list of names available for these frogs. He suggested that several names until then considered as synonyms or as subspecific names did apply to some of these species, and that other species remained to be named. We will provide elsewhere (DUBOIS & OHLER, in preparation) an updated review of the taxonomy of this group. Here we will only extend the discussion to the names which may still pose nomenclatural problems in relation with the existence of two distinct species of this complex in Java.

Following DUBOIS's (1984*b*) paper, few names remained as genuine synonyms of *Rana limnocharis*. However, ZHAO & ADLER (1993: 144) still regarded the name *Rana gracilis* Wiegmann, 1834 as a synonym of the latter. This synonymy deserves discussion. Besides, we discuss here the status of four additional names: *Rana cancrivora* Gravenhorst, 1829; *Rana vittigera* Wiegmann, 1834, *Rana multistriata* Hallowell, 1861, and *Rana wasl* Annandale, 1917.

THE STATUS OF THE NAME *RANA CANCRIVORA* GRAVENHORST, 1829

In contrast with most of other names concerning frogs of this complex, the name *Rana cancrivora* has long been considered to apply to a species distinct from *Rana limnocharis*, e.g. by BOULENGER (1920*a*: 23), VAN KAMPEN (1923: 170), SMITH (1927: 205; 1930: 96), BOURRET (1942: 245), TAYLOR (1962: 377), ZHAO & ADLER (1993: 140), or even INGER (1954: 260; 1966: 175), who provided comparisons between *Rana cancrivora* and *Rana "limnocharis" vittigera*. The fact that *R. cancrivora* was almost universally considered distinct from *R. limnocharis* rests apparently only on the comparative diagnosis provided by GRAVENHORST (1829) for these two species, where this author stated that the former was "larger" than the latter: since then, the name *Rana cancrivora* has been consistently applied to a large species of this complex, occurring in Java and neighbouring regions. However this action has never been based on the examination of a type specimen, and apparently until now no author has tried to trace such a specimen.

An incidental result of the above work is the verification that all type-specimens of species described as new by GRAVENHORST (1829), including *Rana cancrivora*, must now be

considered lost. Gravenhorst (1829) himself considered the names *Rana limnocharis* and *Rana cancrivora* as synonyms, so that unequivocal allocation of the name *Rana cancrivora* to a biological species also requires designation of a neotype. None of the collections mentioned above is known to harbour any specimen under the name *Rana cancrivora* collected near Buitenzorg in Java by Kuhl and/or Van Hasselt. Consequently, another specimen is described below as neotype. For this, we chose a specimen in good condition, collected recently in a precise locality near Bogor and that belongs to the species traditionally recognised under this name. This specimen is part of those that were used as outgroup in the molecular study of this group reported by Veith et al. (2000). Designation of this specimen as neotype of *Rana cancrivora* Gravenhorst, 1829 will preclude any confusion in the allocation of this name to a biological species.

The status of the name *Rana vittigera* Wiegmann, 1834

Wiegmann (1834: 255-257, pl. 21 fig. 1) described *Rana vittigera*, provided a good drawing of a specimen, and compared this new species to *Rana limnocharis*. Subsequently, the species *Rana vittigera* was considered as a synonym of *Rana tigerina* Daudin, 1802 by some authors (e.g. Stejneger, 1907: 139) and of *Rana cancrivora* Gravenhorst, 1829 by others (e.g., Boulenger, 1920*a*: 23), until Taylor (1920: 236) resurrected this name for a species of the Philippines. He was followed by Smith (1927: 205-207) and Inger (1954: 267), who however reduced this taxon to the rank of a subspecies of *Rana limnocharis*. None of these authors examined the type-specimens of this taxon. Inger (1954: 267) stated that its type-locality was "Laguna de Bay, Luzon", which was incorrect because, as noted by Taylor (1920: 236), the species had been described on the basis of specimens from two different origins.

As a matter of fact, according to Wiegmann (1834: 257), the original description was based on several specimens, some from Laguna de Bay (Luzon, Philippines), and some from the market of Macao (now Aomen, Guangdong, China). Peters (1863: 77) provided more information in this respect: he stated that the Berlin Museum had two specimens (ZMB 3269) from Laguna de Bay and two others (ZMB 3270) from China. Dubois (1984*b*: 151-152) commented on this and restricted the type-locality of the species to Laguna de Bay. His comment was misunderstood by Duellman (1993: 229), who wrote: "Lectotypes: ZMB 3269, designated by Dubois, 1984, Alytes, 3: 152." In fact, Dubois (1984*b*: 152) had not designated a lectotype, but had stated that such a designation *should* be made, *after* examination of the specimens: "In order to stabilize definitely the use of the name *vittigera* as proposed by Inger (1954), it would be necessary to designate formally one of the two specimens ZMB 3269 as lectotype of *Rana vittigera* Wiegmann, 1835, what I cannot do for the time being, as I have not yet been able to examine these specimens." (translated from the French text in Dubois, 1984*b*: 152). Because of this misunderstanding, Duellman (1993) "almost" designated a lectotype for this species, but of course he did not, because, to be valid, a lectotype designation must point to an individual, and ZMB 3269 consists of two specimens.

On 21 December 1995, thanks to the hospitality of Rainer Günther, we had the opportunity to examine the 4 known syntypes of this species in the Berlin Museum. When we got the bottles containing these specimens for examination, these bottles were still sealed with resin and had to be cut open with a scalpel, thus emitting a very pleasant smell of old

aromatized alcohol. it is very likely that these specimens had never been examined since the 19th century, perhaps since PETERS's (1863) work.

These four specimens are in good condition. The two specimens from Laguna de Bay, ZMB 3269, are two adult females (SVL 68 6 mm and 57.2 mm) The two specimens from Macao, ZMB 3270, are also two adult females (SVL 58.5 mm and 55 9 mm). Comparisons of these four specimens with fig 1 of pl. 1 of WIEGMANN (1834) shows that the latter was drawn from the largest of the two specimens from Laguna de Bay. This specimen is therefore here designated as lectotype of *Rana vittigera*, which is consistent with the use of this name introduced by TAYLOR (1920) and adopted by all subsequent authors. This lectotype is described in detail and figured below.

THE STATUS OF THE NAME *RANA GRACILIS* WIEGMANN, 1834

WIEGMANN (1834: 257-258) described *Rana gracilis* on the basis of a single adult male specimen, collected in China near the "Cap Syng-more" (now Kap Shui Mun, Lantau Island, Hong Kong, China). He considered this species as very close to *Rana limnocharis*. PETERS (1863: 78) stated that this species was "completely identical" ("stimmt ganz uberein") with *Rana limnocharis* and *Rana vittigera*. Since then, all authors have considered the name *Rana gracilis* Wiegmann, 1834 as a subjective synonym of *Rana limnocharis*, and this synonymy was still considered valid by ZHAO & ADLER (1993: 144), who however did not include *Rana vittigera* in this synonymy.

During our stay in Berlin mentioned above, we examined the holotype of this species, ZMB 3255. We provide below a redescription and a photograph of this specimen. We consider that, by several important characters, this specimen is distinct from both species of this group known from Java. frogs from China have significantly shorter heads, forelegs and hindlimbs, and their inner metatarsal tubercle is shorter relative to the length of first toe We will provide more information on this question elsewhere, but, for the purpose of this paper, it is enough to say that this Chinese species is distinct from both Javanese species of this group, and should be removed from the synonymy of *Rana limnocharis*. This statement is also supported by the results of the electrophoretic comparison of specimens froms Java and Hong Kong (TODA et al., 1998).

However, the name *Rana gracilis* Wiegmann, 1834 cannot be resurrected for this Chinese species, because this name is preoccupied in the genus *Rana* (see e g DUBOIS, 1984*b* 154), being a junior primary homonym of the name *Rana gracilis* Gravenhorst, 1829, a Sri Lankan species of the subgenus *Sylvirana* Dubois, 1992 of the genus *Rana* Linnaeus, 1758 (see DUBOIS, 1992 326) According to the *Code*, a junior primary homonym is permanently invalid, so that the name *Rana gracilis* cannot be resurrected for the Chinese species, even if the two species bearing this name are no longer considered congeneric As no junior synonym of this name is currently known (see e g ZHAO & ADLER, 1993 144), it would seem that we are in a situation where, to designate this Chinese species, a new replacement name (nomen novum) should be coined for the name *Rana gracilis* Wiegmann, 1834 However, we propose below another, more "parsimonious", solution to this problem.

THE STATUS OF THE NAME *RANA MULTISTRIATA* HALLOWELL, 1861

In a long and famous paper, HALLOWELL (1861) described several amphibian species from Japan and Hong Kong. Several of these nominal species have never been allocated to biological species since then, and their types seem to be lost (see e.g. ZHAO & ADLER, 1993: 280). However, these names are nomenclaturally available and their status should be clarified, which can be done through the designation of neotypes from the same localities (see e.g. DUBOIS & OHLER, 1997*a-b*). To be sure, HALLOWELL's (1861) descriptions are too vague to allow unambiguous allocation of these names. In order not to threaten the stability of nomenclature, we think allocation of these names should be done following the three following principles: (1) the biological species to which the name is allocated should be known to be present in the area whence HALLOWELL's specimens came; (2) it should not have characters incompatible with HALLOWELL's (1861) description; (3) this species should either be still unnamed or be known under a name published before 1861, so that HALLOWELL's name becomes its junior subjective synonym. in the latter case, HALLOWELL's name would remain available for further taxonomic work, for example if a frog species from Hong Kong, currently considered conspecific with other populations, was later shown to be a different species.

In the light of these ideas, we propose the following interpretations of the three species names proposed by HALLOWELL (1861) for frogs of Hong Kong, and which ZHAO & ADLER (1993: 280) kept unallocated to biological species: *Rana trivittata*, *Rana nebulosa* and *Rana multistriata*.

(1) Concerning the name *Rana trivittata*, in the light of the original description (HALLOWELL, 1861: 504-505), we consider that it could well apply to the species now known as *Rana macrodactyla* (Günther, 1859), a member of the subgenus *Hylarana* Tschudi, 1838 of the genus *Rana* (see DUBOIS, 1992: 328), which occurs in Hong Kong (LAI & NG, 1972; KARSEN et al., 1986). Definitive stabilization of the status of *Rana trivittata* as a junior subjective synonym of *Rana macrodactyla* will require the designation as neotype of *R. trivittata* of a specimen of the latter species collected in Hong Kong.

(2) As for the name *Rana nebulosa*, examination of the original description (HALLOWELL, 1861: 505) leads us to think that it could fit the species currently known as *Rana livida* (Blyth, 1856), a species currently placed either in the subgenus *Odorrana* Fei, Ye & Huang, 1991 or in the subgenus *Eburana* Dubois, 1992 of the genus *Rana* (see FEI et al., 1991: 147; DUBOIS, 1992: 328; FEI, 1999: 188), which also occurs in Hong Kong (LAI & NG, 1972; KARSEN et al., 1986). In this case also, stabilization of this name in this synonymy will require the designation of a neotype from Hong Kong.

(3) Finally, HALLOWELL's (1861: 504-505) original description of the species *Rana multistriata* could well apply to a species of the *Rana limnocharis* group, which is also present in Hong Kong. As we have seen above, the holotype of *Rana gracilis* Wiegmann, 1834, collected in Hong Kong, belongs to a species distinct from *Rana limnocharis*, and for which no scientific name is currently available. We propose to take advantage of this situation to apply the name *Rana multistriata* to this unnamed Chinese frog species, through designation as

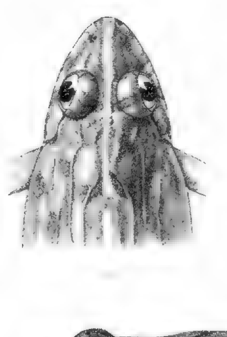
neotype of the latter of the holotype of *Rana gracilis*, described and figured below: this solution of the nomenclatural problems posed by both these names is an example of "nomenclatural parsimony", a concept that will be discussed at more length elsewhere (DUBOIS, in preparation).

THE STATUS OF THE NAME *RANA WASL* ANNANDALE, 1917

ANNANDALE (1917: 131-132) erected the species *Rana wasl* for specimens from various regions (Sarawak, Myanmar, Assam & Nicobar Islands). He stated that the holotype, ZSI 17282, was from Kuching (Sarawak, Malaysia, in the island of Borneo). BOULENGER (1920*a*: 28) placed this name in the synonymy of *Rana limnocharis*, where it has remained until now (e.g.: VAN KAMPEN, 1923: 167, BOURRET, 1942: 250, GORHAM, 1974: 146), except for authors who failed to mention it (e.g.: LIU, 1950: 315; TAYLOR, 1962: 380; INGER, 1966: 205). On 14 August 1973, DUBOIS (1984*b*: 155) was able to examine and measure the holotype of *Rana wasl* in the Calcutta Museum. it is an adult female (SVL 56 mm; TL 31 mm; HW 19 mm; HL 18.5 mm; IUE 3 mm, UEW 4.5 mm; IN 5 mm), which is quite accurately shown in fig. 5 and 5a of pl. 5 of ANNANDALE (1917), here reproduced as fig. 1. We are unable to provide here a full redescription of this holotype, as the current loan policy of the Zoological Survey of India of Calcutta is to refuse to send specimens abroad (Indraneil Das, e-mail to AD of 29 October 1998).

GENERIC CLASSIFICATION

A few words must be said here about the generic classification of the frogs related to *Rana limnocharis*. Although long maintained in the genus *Rana* Linnaeus, 1758 (the type-species of which is the European *Rana temporaria* Linnaeus, 1758: see DUBOIS, 1992: 333), these species have often been referred to a particular "group", "complex", "section" or "subgenus" of this genus. Thus, ANNANDALE (1917: 131) placed them in a "*Rana limnocharis* group", which he considered distinct from a "*Rana tigrina* group". In contrast, BOULENGER (1918: 115) united both groups in a "groupe de *R. tigrina* et *limnocharis*" of his subgenus *Rana* s. str., he later considered the same group as a "section" "*Ranae tigrinae*" of this genus (BOULENGER, 1920*a*: 9). DECKERT (1938) placed these species, as well as others, in the genus *Dicroglossus* Gunther, 1860, which was recognized as a valid genus by LAURENT (1950), and later by DUBOIS (1974), but as a subgenus of *Rana*. DUBOIS (1975*a*: 1112) pointed out that, for the latter group, the name *Euphlyctis* Fitzinger, 1843 had priority. DUBOIS (1981: 238-240) recognized several species groups in the latter subgenus and designated *Rana limnocharis* as type-species of *Fejervarya* Bolkay, 1915, in order to provide a genus-group name for this group. DUBOIS (1984*b*) proposed to use this latter name as a subgeneric name within *Rana*. DUBOIS (1987: 61) transferred this subgenus to the genus *Limnonectes* Fitzinger, 1843. Finally, FEI et al. (1991: 126) were the first to raise the *Rana limnocharis* group to the rank of a distinct genus, for which, however, they used the incorrect name *Euphlyctis* (which applies in fact to *Rana cyanophlyctis* Schneider, 1799 and related species, i.e. a quite distinct group indeed: see DUBOIS, 1992). DUBOIS (2000), ISKANDAR (1998, 1999), FEI (1999) and MARMAYOU et al. (2000) followed this suggestion, except for its nomenclatural part, since *Fejervarya* is the valid name for this group.



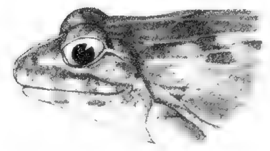


Fig. 1. – *Rana wasl* Annandale, 1917, holotype, ZSI 17282: head in dorsal and lateral view (reproduced from fig. 5 and 5a of pl. 5 of Annandale, 1917).

Several reasons lead us to adopt Fei et al.'s (1991) proposal. This decision is supported both by the important phenetic differences that exist between *Fejervarya* and *Limnonectes*, such as the shape of the tips of digits of adults (Ohler & Dubois, 1999), their types of male secondary characters (Boulenger, 1920*a*), a higher morphometrical distance between the adults of these genera than between them and those of other genera such as *Phrynoglossus* Peters, 1867 (Ohler & Dubois, 1999), or the differences in the mouthparts of their tadpoles (Fei et al., 1991). More significantly even, the preliminary cladistic analyses, based on DNA sequencing, provided independently by Vences (1999), Marmayou et al. (2000) and Bossuyt

& MILINKOVITCH (2000), suggest that *Fejervarya* is not the sister-group of *Limnonectes*, but is more closely related to other genera such as *Hoplobatrachus* Peters, 1863 and *Sphaerotheca* Gunther, 1859.

For all these reasons, we refer here all the species of the former "*Rana limnocharis* group" to a distinct genus *Fejervarya* Bolkay, 1915. We take this opportunity to point out the presence in all species of this genus of a unique common derived character which seems to have escaped the attention of all authors until now. This character was observed by us in all examined species of this genus, but not in any other of a vast array of ranids from various groups examined in this respect by us and also by Julio Mario Hoyos (personal communication). In species of the genus *Fejervarya*, the ventro-lateral edge of the *musculus pectoralis pars abdominalis* is slightly attached to the skin from armpit to groin, whereas usually in ranids it is attached to muscles which are dorsal relative to it (*musculus rectus abdominis* and *musculus obliquus externus*). This results in the presence, in adults of both sexes of all species of *Fejervarya*, of a dark ventro-lateral line from armpit to groin, which is usually very clearly conspicuous in live specimens, whose belly in this genus is usually bright white or yellowish and unspotted. This dark line being characteristic of the species of the genus *Fejervarya*, we propose to call it the "Fejervaryan line" We consider this character as an autapomorphy of the genus *Fejervarya*, that provides an apognosis for this genus (see DUBOIS, 1997)

This genus is still in need of an overall revision For the time being, on the basis of the information already published by DUBOIS (1984*b*, 1987, 1992) and provided in the present paper, we recognize the following species as valid: *Fejervarya andamanensis* (Stoliczka, 1870); *Fejervarya cancrivora* (Gravenhorst, 1829), *Fejervarya greenii* (Boulenger, 1904), *Fejervarya keralensis* (Dubois, 1981) [synonym: *Rana verrucosa* Gunther, 1876]; *Fejervarya kirtisinghei* (Manamendra-Arachchi & Gabadage, 1996), *Fejervarya limnocharis* (Gravenhorst, 1829) [synonyms: *Rana limnocharis* Wiegmann, 1834 and *Rana wasl* Annandale, 1917], *Fejervarya multistriata* (Hallowell, 1861) [synonym *Rana gracilis* Wiegmann, 1834], *Fejervarya nepalensis* (Dubois, 1975), *Fejervarya nilagirica* (Jerdon, 1853), *Fejervarya pierrei* (Dubois, 1975), *Fejervarya rufescens* (Jerdon, 1853), *Fejervarya syhadrensis* (Annandale, 1919); *Fejervarya teraiensis* (Dubois, 1984), *Fejervarya vittigera* (Wiegmann, 1834) Besides, the following names, which are still unsufficiently characterized in published works, will also have to be considered in any global revisionary work of this genus. *Fejervarya altilabris* (Blyth, 1855), *Fejervarya assimilis* (Blyth, 1852), *Fejervarya brama* (Lesson, 1834); *Fejervarya brevipalmata* (Peters, 1871); *Fejervarya frithi* (Theobald, 1868); *Fejervarya moodiei* (Taylor, 1920), *Fejervarya murthii* (Pillai, 1979); *Fejervarya mysorensis* (Rao, 1922), *Fejervarya nicobariensis* (Stoliczka, 1870), *Fejervarya parambikulamana* (Rao, 1937); *Fejervarya pulla* (Stoliczka, 1870), *Fejervarya raja* (Smith, 1930), *Fejervarya sauriceps* (Rao, 1937), *Fejervarya schlueteri* (Werner, 1893); *Fejervarya verruculosa* (Roux, 1911).

Descriptions of type-specimens

Neotype, by present designation, of *Rana limnocharis* Gravenhorst, 1829 and of *Rana limnocharis* Wiegmann, 1834 (fig. 2-3)

RMNH 4287, young female, collected by H. Kuhl in 1821 near Buitenzorg [now Bogor] (06°35'S, 106°47'E), West Java, Java, Indonesia.

(A) Size and general aspect. – (1) Specimen of medium size (SVL 44.4 mm), body rather slender.

(B) Head. – (2) Head of medium size, wider (HW 16.0 mm) than long (HL 14.6 mm; MN 13.6 mm, MFE 9.8 mm; MBE 6.2 mm), convex. (3) Snout oval, protruding, its length (SL 7.78 mm) longer than horizontal diameter of eye (EL 5.19 mm). (4) Canthus rostralis rounded, loreal region concave, acute. (5) Interorbital space flat, smaller (IUE 2.20 mm) than upper eyelid (UEW 3.89 mm) and internarial distance (IN 3.05 mm); distance between front of eyes (IFE 6.3 mm) more than one half of distance between back of eyes (IBE 10.9 mm). (6) Nostrils oval, with small lateral flap, closer to tip of snout (NS 2.46 mm) than to eye (EN 4.02 mm). (7) Pupil rounded. (8) Tympanum (TYD 2.92 mm) distinct, oval, horizontal, about half of eye diameter; tympanum-eye distance (TYE 1.55 mm) about half its diameter. (9) Pineal ocellus present, between anterior border of eyes. (10) Vomerine ridge present, bearing few small teeth, between choanae, with an angle of 45° to body axis, closer to choanae than from each other, longer than distance between them. (11) Tongue large, cordate, emarginate. (12) Supratympanic fold distinct, from eye to shoulder. (13) Parotoid glands absent. (14) Cephalic ridges absent. (15) Co-ossified skin absent.

(C) Forelimbs. – (16) Arm short, rather thin (FLL 8.7 mm), shorter than hand (HAL 9.8 mm), not enlarged. (17) Fingers long, thin (TFL 5.77 mm). (18) Relative length of fingers, shortest to longest: II < IV < I < III. (19) Tips of fingers pointed. (20) Fingers without dermal fringe, webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present. (22) Prepollex oval, prominent; two oval, flat palmar tubercles; supernumerary tubercles absent.

(D) Hindlimbs. – (23) Shank almost four times longer (TL 23.6 mm) than wide (TW 6.6 mm), longer than thigh (FL 20.6 mm), but shorter than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 24.6 mm). (24) Toes long, thin; toe IV long (FTL 14.4 mm), more than one third of distance from base of tarsus to tip of toe IV (TFOL 36.1 mm). (25) Relative length of toes, shortest to longest: I < II < V – III < IV. (26) Tips of toes pointed. (27) Webbing moderate: I 1 – 2 II 1 – 2 III 1 – 2 $^{2}/_{3}$ IV 2 $^{2}/_{3}$ – 1 $^{1}/_{2}$ V (WTF 4.80 mm, WFF 4.54 mm, WI 3.69 mm; WII 3.50 mm, MTTF 12.2 mm, MTFF 12.2 mm; TFTF 11.8 mm, FFTF 12.8 mm). (28) Dermal fringe along toe V present, from tip of toe to base of metatarsus, well developed. (29) Subarticular tubercles prominent, rounded, simple, all present. (30) Inner metatarsal tubercle rather short, prominent, its length (IMT 2.14 mm) more than 2.5 times in length of toe I (ITL 5.57 mm). (31) Inner tarsal ridge present on distal third of tarsus. (32) Outer metatarsal tubercle absent, supernumerary tubercles absent; tarsal tubercle absent.



Fig. 2. – *Rana limnocharis* Gravenhorst, 1829, neotype, and *Rana limnocharis* Wiegmann, 1834, neotype. RMNH 4287, young female (SVL 44.4 mm): dorsal view.

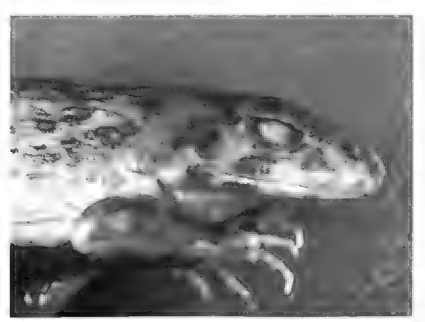


Fig. 3. – *Rana limnocharis* Gravenhorst, 1829, neotype, and *Rana limnocharis* Wiegmann, 1834, neotype. RMNH 4287, young female (SVL 44.4 mm): right lateral view of head.

(E) Skin – (33) Dorsal and lateral parts of head and body, snout and between the eyes smooth; side of head with few glandular warts; back and upper part of flanks with glandular folds; lower part of flanks with glandular warts. (34) Latero-dorsal folds absent. (35) Dorsal parts of limbs, forelimbs smooth; thigh and shank with glandular warts; tarsus smooth. (36) Ventral parts of head, body and limbs: throat, chest and belly smooth, thigh with glandular warts. (37) No macroglands.

(F) Coloration in alcohol. – (38) Dorsal and lateral parts of head and body, fawn with a large dirty-white mid-dorsal band and darker brown spots; upper flank coffee brown with darker spots, lower part light fawn, loreal and temporal region fawn with a brown band on canthus rostralis and tympanic fold and brown spots on upper lip; tympanum light fawn with its dorsal half dark brown. (39) Dorsal parts of limbs: forelimbs, thigh, shank and foot fawn with darker bands; posterior part of thigh brown with white marbling. (40) Ventral parts of head, body and limbs: throat, chest, belly and thigh light fawn; margin of throat light fawn white with large brown spots; Fejervaryan line present.

(G) Female sexual characters. – (41) Oviduct translucent, folded. (42) Ovaries not observed.

NEOTYPE, BY PRESENT DESIGNATION, OF *RANA CANCRIVORA* GRAVENHORST, 1829 (FIG. 4-5)

FMNH 256688 (field number MV40), adult male, collected by Michael Veith on 5 February 1993 at Cianjur (06°49'S, 107°08'E), West Java, Java (Indonesia).

(A) Size and general aspect. – (1) Specimen of rather large size (SVL 68.2 mm), body rather slender.

(B) Head. – (2) Head of medium size, narrower (HW 26.0 mm) than long (HL 29.7 mm, MN 27.2 mm; MFE 21.3 mm; MBE 15.6 mm), slightly convex. (3) Snout oval, protruding, its length (SL 10.9 mm) longer than horizontal diameter of eye (EL 7.7 mm). (4) Canthus rostralis rounded, loreal region concave, obtuse. (5) Interorbital space flat, smaller (IUE 3.3 mm) than upper eyelid (UEW 5.5 mm) and internarial distance (IN 4.4 mm); distance between front of eyes (IFE 9.9 mm) more than one half of distance between back of eyes (IBE 15.8 mm). (6) Nostrils oval, with small lateral flap, closer to tip of snout (NS 5.4 mm) than to eye (EN 6.9 mm). (7) Pupil rounded. (8) Tympanum (TYD 4.8 mm) distinct, oval, horizontal, about two thirds of eye diameter, tympanum-eye distance (TYE 2.7 mm) about half its diameter. (9) Pineal ocellus present, between anterior quarter of eyes. (10) Vomerine ridge present, bearing a few small teeth, between choanae, with an angle of 45° to body axis, closer to choanae than from each other, longer than distance between them. (11) Tongue large, cordate, emarginate. (12) Supratympanic fold distinct, from eye to shoulder. (13) Parotoid glands absent. (14) Cephalic ridges absent. (15) Co-ossified skin absent.

(C) Forelimbs. – (16) Arm short, rather thin (FLL 15.8 mm), slightly longer than hand (HAL 15.3 mm), not enlarged. (17) Fingers rather long, thin (TFL 7.9 mm). (18) Relative length of fingers, shortest to longest: II < IV < I < III. (19) Tips of fingers pointed. (20) Fingers II and III with dermal fringe, webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present. (22) Prepollex oval, indistinct, palmar tubercles indistinct, supernumerary tubercles absent.



Fig. 4. – *Rana cancrivora* Gravenhorst, 1829, neotype, FMNH 256688, adult male (SVL 68.2 mm): dorsal view.

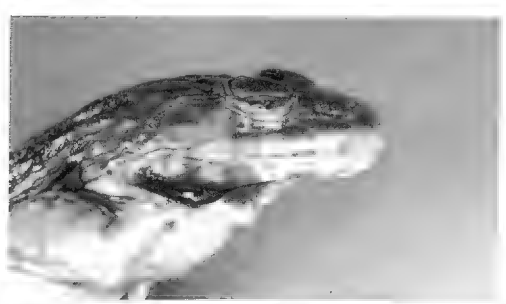


Fig. 5. – *Rana cancrivora* Gravenhorst, 1829, neotype, FMNH 256688, adult male (SVL 68.2 mm): right lateral view of head.

(D) Hindlimbs. – (23) Shank about three times longer (TL 35.7 mm) than wide (TW 12.9 mm), longer than thigh (FL 33.6 mm), but shorter than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 37.8 mm). (24) Toes long, thin; toe IV long (FTL 21.6 mm), more than one third of distance from base of tarsus to tip of toe IV (TFOL 52.9 mm). (25) Relative length of toes, shortest to longest: I < II < V < III < IV. (26) Tips of toes pointed. (27) Webbing moderate: I 1 – 1 ½ II 1 – 2 III 1 – 2 IV 2 – 1 V (WTF 7.0 mm, WFF 7.3 mm, WI 6.7 mm, WII 5.3 mm). (28) Dermal fringe along toe V present, from tip of toe to base of metatarsus, well developed. (29) Subarticular tubercles prominent, oval, simple, all present. (30) Inner metatarsal tubercle oval, prominent, its length (IMT 3.7 mm) less than 2.5 times length of toe I (ITL 8.8 mm). (31) Inner tarsal ridge present on distal $^{2}/_{3}$ of tarsus. (32) Outer metatarsal tubercle absent, supernumerary tubercles absent; tarsal tubercle absent.

(E) Skin. – (33) Dorsal and lateral parts of head and body: snout and between the eyes shagreened; side of head with small glandular warts; back and upper part of flanks with glandular folds, lower part of flanks with glandular warts. (34) Fine, narrow, interrupted latero-dorsal folds on $^{2}/_{3}$ of back. (35) Dorsal parts of limbs: forelimbs, thigh, shank and tarsus with glandular warts and folds. (36) Ventral parts of head, body and limbs: throat, chest and belly smooth. (37) No macroglands.

(F) Coloration in alcohol. – (38) Dorsal and lateral parts of head and body: brown with indistinct darker brown spots around the folds, canthus rostralis and tympanic fold of same brown color; tympanum brown with inferior half clearer, lighter than head, three wide bands from eye to upper lip, a wide light brown mid-dorsal band continuous from tip of snout to vent. (39) Dorsal parts of limbs: forelimbs, thigh, shank and foot brown with darker bands; posterior part of thigh dark brown with white marbling. (40) Ventral parts of head, body and limbs: throat light brown with dark brown vocal sacs on both sides; belly and underside of shank white with indistinct light brown spots; margin of throat white with large brown spots; Fejervaryan line not visible (specimen dissected).

(G) Male sexual characters. – (41) Unique pad of numerous small grey brown nuptial spines on prepollex and finger I. (42) Vocal sacs present.

Lectotype, by present designation, of *Rana vittigera* Wiegmann, 1834 (fig. 6-8)

Largest of the two specimens under number ZMB 3269, adult female, collected by F. J. F. Meyen in Laguna de Bay (14°10'N, 121°20'E), Luzon, Philippines.

(A) Size and general aspect. – (1) Specimen rather large size (SVL 68.6 mm), body rather slender.

(B) Head. – (2) Head of medium size, narrower (HW 21.6 mm) than long (HL 24.6 mm, MN 21.1 mm, MFE 16.0 mm, MBE 9.8 mm), convex. (3) Snout oval, protruding, its length (SL 10.1 mm) longer than horizontal diameter of eye (EL 7.2 mm). (4) Canthus rostralis rounded, loreal region concave, obtuse. (5) Interorbital space flat, smaller (IUE 3.70 mm) than upper eyelid (UEW 5.23 mm) and internarial distance (IN 3.63 mm), distance between front of eyes (IFE 9.5 mm) two thirds of distance between back of eyes (IBE 13.8 mm). (6) Nostrils oval, closer to tip of snout (NS 4.40 mm) than to eye (EN 5.93 mm). (7) Pupil indistinct. (8) Tympanum (TYD 4.61 mm) distinct, oval, horizontal, about half of eye diameter.

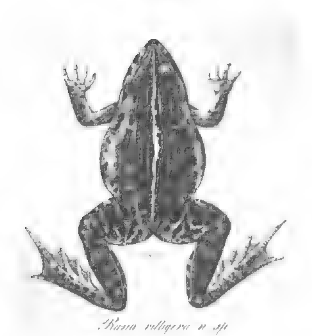


Fig 6 – *Rana vittigera* Wiegmann, 1834, lectotype, largest of the two specimens under number ZMB 3269: dorsal view (reproduced from fig. 1 of pl 21 of WIEGMANN, 1834)

tympanum-eye distance (TYE 2 44 mm) about half its diameter. (9) Pineal ocellus present, between anterior border of eyes. (10) Vomerine ridge present, bearing few small teeth, between choanae, with an angle of 45° to body axis, closer to choanae as from each other, longer than distance between them (11) Tongue not observed (12) Supratympanic fold distinct, from eye to shoulder. (13) Parotoid glands absent (14) Cephalic ridges absent. (15) Co-ossified skin absent

(C) Forelimbs. - (16) Arm short, rather thin (FLL 12 6 mm), about as long as hand (HAL 12 3 mm), not enlarged (17) Fingers rather long, thin (TFL 7 0 mm) (18) Relative length of fingers, shortest to longest IV < II < I < III (19) Tips of fingers pointed (20) Fingers without dermal fringe, webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present. (22) Prepollex oval, indistinct, two oval, flat palmar tubercles; supernumerary tubercles absent

(D) Hindlimbs. (23) Shank three times longer (TL 31 4 mm) than wide (TW 11 4 mm), thigh (FL not measured, femur broken) about distance from base of internal metatarsal tubercle to tip of toe IV (FOL 31 6 mm) (24) Toes rather short, thin; toe IV long (FTL 11 9 mm), less than one third of distance from base of tarsus to tip of toe IV (TFOL 46 5 mm). (25) Relative length of toes, shortest to longest. I < II < V = III < IV (26) Tips of toes pointed (27) Webbing extensive I 0 – 1 II 0 – 1½ III 0 – 1½ IV 1½ – 0 V (WTF 8 3 mm, WFF 6 6 mm,



Fig. 7. – *Rana vittigera* Wiegmann, 1834, lectotype, largest of the two specimens under number ZMB 3269, adult female (SVL 68.6 mm): dorsal view.

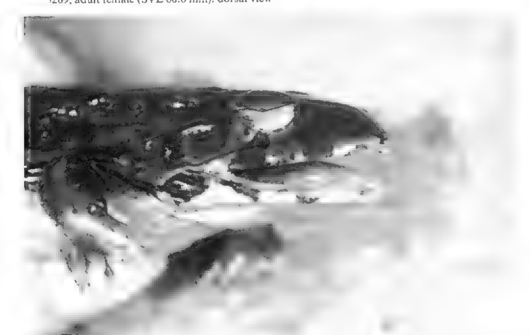


Fig. 8. – *Rana vittigera* Wiegmann, 1834, lectotype, largest of the two specimens under number ZMB 3269, adult female (SVL 68.6 mm), right lateral view of head.

WI 7.2 mm, WII 4.8 mm; MTTF 16.6 mm; MTFF 17.4 mm; TFTF 12 9 mm; FFTF 13 8 mm). (28) Dermal fringe along toe V present, from tip of toe to base of metatarsus, slightly developed. (29) Subarticular tubercles prominent, oval, simple, all present (30) Inner metatarsal tubercle short, very prominent; its length (IMT 2.23 mm) more than 3.5 times in length of toe I (ITL 8.16 mm). (31) Inner tarsal ridge absent. (32) Outer metatarsal tubercle absent; supernumerary tubercles absent; tarsal tubercle absent.

(E) Skin - (33) Dorsal and lateral parts of head and body. snout and between the eyes smooth; side of head with few glandular warts, back and upper part of flanks with short and long glandular folds (the longest half of length of back); lower part of flanks with faded glandular warts. (34) Latero-dorsal folds absent. (35) Dorsal parts of limbs: forelimbs smooth; thigh with glandular warts and horny spinules; shank and tarsus smooth (36) Ventral parts of head, body and limbs: throat, chest and belly smooth, thigh with glandular warts. (37) No macroglands.

(F) Coloration in alcohol (38) Dorsal and lateral parts of head and body brown with large, dense darker brown, rounded, confluent spots; light mid-dorsal line, slightly broadened to the right in the mid of the back, shoulder pads continued by a clear band on the flanks; three dark spots on upper lip, canthus rostralis and tympanic zone dark brown. (39) Dorsal parts of limbs. forelimbs, thigh, shank and foot brown with outlines of darker bands, posterior part of thigh dark brown with white marbling. (40) Ventral parts of head, body and limbs: throat, chest, belly and thigh dirty white; margin of throat with some brown spots, Fejervaryan line present.

(G) Female sexual characters. (41) Oviduct large, folded (42) Ovaries with small brown and whitish eggs.

HOLOTYPE, BY MONOTYPY, OF *RANA GRACILIS* WIEGMANN, 1834 (NEC GRAVENHORST, 1829) AND NEOTYPE, BY PRESENT DESIGNATION, OF *RANA MULTISTRIATA* HALLOWELL, 1861 (FIG. 9-10)

ZMB 3255, adult male, collected by F J F Meyen near "Cap Syng-more", now Kap Shui Mun (22°21'N, 114°03'E), Lantau Island, Hong Kong, China

(A) Size and general aspect (1) Specimen of rather small size (SVL 33.0 mm), body rather slender

(B) Head - (2) Head of medium size, longer (HL 12 6 mm) than wide (HW 10 0 mm; MN 10 8 mm, MFE 8 2 mm, MBE 4 4 mm), convex. (3) Snout oval, slightly protruding, its length (SL 5.44 mm) longer than horizontal diameter of eye (EL 4 61 mm) (4) Canthus rostralis rounded, loreal region concave, obtuse (5) Interorbital space flat, smaller (IUE 1 73 mm) than upper eyelid (UEW 2 74 mm) and internarial distance (IN 2 33 mm), distance between front of eyes (IFE 5.5 mm) more than two thirds of distance between back of eyes (IBE 7 6 mm) (6) Nostrils oval, closer to tip of snout (NS 2.00 mm) than to eye (EN 2 80 mm) (7) Pupil rounded (8) Tympanum (TYD 2 04 mm) distinct, oval, horizontal, about half of eye diameter, tympanum-eye distance (TYE 0 67 mm) about one third its diameter. (9) Pineal ocellus absent (10) Vomerine ridge present, bearing few small teeth, between choanae, with an angle of 45° to body axis, less close to choanae than from each other, longer than distance



Fig. 9. - *Rana gracilis* Wiegmann, 1834, holotype, and *Rana multistriata* Hallowell, 1861, neotype, ZMB 3255, adult male (SVL 33.0 mm): dorsal view.

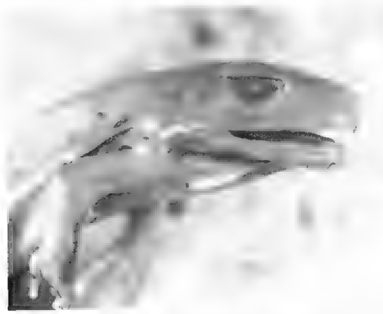


Fig. 10. - *Rana gracilis* Wiegmann, 1834, holotype, and *Rana multistriata* Hallowell, 1861, neotype, ZMB 3255, adult male (SVL 33.0 mm): right lateral view of head.

between them. (11) Tongue not observed (12) Supratympanic fold indistinct, from eye to shoulder. (13) Parotoid glands absent (14) Cephalic ridges absent. (15) Co-ossified skin absent

(C) Forelimbs. - (16) Arm short, rather thin (FLL 6.4 mm), shorter than hand (HAL 7.5 mm), not enlarged. (17) Fingers long, thin (TFL 4.33 mm). (18) Relative length of fingers, shortest to longest: IV < II < I < III. (19) Tips of fingers rounded. (20) Fingers without dermal fringe, webbing absent. (21) Subarticular tubercles prominent, rounded, single, all present. (22) Prepollex oval, prominent; one round, distinct internal palmar tubercle beside a very small external palmar tubercle; supernumerary tubercles absent.

(D) Hindlimbs. (23) Shank four times longer (TL 15 8 mm) than wide (TW 3.5 mm), longer than thigh (FL 14.1 mm), but shorter than distance from base of internal metatarsal tubercle to tip of toe IV (FOL 17 5 mm). (24) Toes long, thin; toe IV long (FTL 10.6 mm), more than one third of distance from base of tarsus to tip of toe IV (TFOL 26.0 mm). (25) Relative length of toes, shortest to longest I < II < V = III < IV. (26) Tips of toes rounded. (27) Webbing moderate: I 1 – 2 II 1 – 2 III 1 ½ – 2 $^{2}/_{3}$ IV 2 $^{2}/_{3}$ – 1 V (WTF 3 35 mm, WFF 3.21 mm; WI 3.10 mm, WII 2.37 mm, MTTF 8.65 mm, MTFF 8 86 mm; TFTF 7 74 mm; FFTF 8.51 mm). (28) Dermal fringe along toe V present, from tip of toe to base of metatarsus, scarcely developed. (29) Subarticular tubercles prominent, oval, simple, all present (30) Inner metatarsal tubercle very short, very prominent, its length (IMT 1.16 mm) almost 4 times in length of toe I (ITL 4 44 mm). (31) Inner tarsal ridge absent. (32) Outer metatarsal tubercle absent; supernumerary tubercles absent; tarsal tubercle absent.

(E) Skin. – (33) Dorsal and lateral parts of head and body snout and between the eyes smooth; side of head with few glandular warts, back and upper part of flanks with rather short glandular folds (the longest about size of eye-length), lower part of flanks almost smooth (34) Latero-dorsal folds absent. (35) Dorsal parts of limbs forelimbs and thigh smooth, shank and tarsus with horny spinules. (36) Ventral parts of head, body and limbs: throat, chest and belly smooth, thigh with glandular warts. (37) No macroglands.

(F) Coloration in alcohol (38) Dorsal and lateral parts of head and body colours faded, brown with a large clearer mid-dorsal band and darker brown spots; shoulder spots indistinct; four brown spots on each side of upper lip. (39) Dorsal parts of limbs forelimbs, thigh, shank and foot with dark bands; posterior part of thigh brown with white net forming a light longitudinal line on the back side of each thigh. (40) Ventral parts of head, body and limbs chest, belly and thigh dirty white, greyish spots on side of throat continuous in the middle; margin of throat beige white with large brown spots, Fejervaryan line present

(G) Male sexual characters. (41) Nuptial spines present, one single patch on prepollex and finger I numerous, very small, cream-coloured spines. (42) Vocal sacs present, greyish, folded skin on the two sides of the throat, slit-like openings in posterior part of mouth floor (43) Fine horny spinules on the anterior border of the throat.

RÉSUMÉ

Une analyse détaillée du statut nomenclatural de l'espèce nominale *Rana limnocharis* montre qu'elle a été rendue disponible pour la première fois par GRAVENHORST (1829), puis

une deuxième fois indépendamment par Wiegmann (1834). Les conséquences de ces faits en ce qui concerne les types porte-noms de ces deux espèces nominales sont discutées et des néotypes sont designés pour celles-ci. Le statut des espèces nominales suivantes, voisines de *Rana limnocharis*, est aussi discuté et leurs spécimens-types sont décrits: *Rana cancrivora* Gravenhorst, 1829; *Rana vittigera* Wiegmann, 1834, *Rana gracilis* Wiegmann, 1834; *Rana multistriata* Hallowell, 1861; *Rana wasl* Annandale, 1917. Finalement, sur la base de plusieurs informations récentes, il est suggéré que le groupe de grenouilles habituellement désigné comme "groupe de *Rana limnocharis*" ou "sous-genre *Fejervarya*" devrait être reconnu comme un genre distinct, *Fejervarya* Bolkay, 1915.

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Dentigerous bones and dentition in the paedomorphic plethodontid salamander *Eurycea neotenes*[1]

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Tooth-bearing bones and dentition of males and females of the paedomorphic plethodontid salamander *Eurycea neotenes* are described using alizarin transparencies and SEM micrographs. Dentition is strictly monostichous at the upper jaw (premaxillae only), the lower jaw (dentaries, splenials) and the palate (vomers, palatopterygoids). Teeth in both sexes are monocuspid, conical, and pedicellate, but the weak zone between the dentine crown and the pedicel is not very distinct and does not progress beyond a late larval stage. In addition, we found some sex-linked characters. Compared with females, males possess stronger premaxillae with separated *processus faciales*, fissured inner margins of the dentated parts of the palatopterygoids that overlap the parasphenoid, and larger splenials bearing more teeth. In addition, males appear to have longer teeth, especially on the anterior portion of premaxillae.

INTRODUCTION

In Urodela, tooth bearing bones, dentition and the form of teeth undergo a more or less specific developmental sequence and remodeling during metamorphosis (WILDER, 1925, STADTMÜLLER, 1924, GREVEN, 1988, CLEMEN & GREVEN, 1977, 1994). Paedomorphic species often possess a mosaic of larval and metamorphic traits which reflect their "degree" of paedomorphosis, such traits can be found also in the tooth systems (e.g., GREVEN & CLEMEN, 1980; CLEMEN & GREVEN, 1988; REILLY 1994).

In plethodontids, paedomorphosis has played a significant role in influencing evolutionary patterns and larval as well as paedomorphic features of the tooth systems have been described (e.g., LARSEN, 1963; WAKE, 1966, MUTZ & CLEMEN, 1992).

1. Dedicated to Prof. Dr H Hartwig, Cologne, on the occasion of his 90th birthday
2. Address for correspondence

In the present paper we examine the lower and upper jaw as well as the palate of the plethodontid *Eurycea neotenes*. This species was considered to be probably paedogenetic (progenetic) and not neotenic (Bruce, 1976; Sweet, 1977; for terminology and the use of the term paedomorphosis to specify any retention of juvenile features by adult descendants, see Gould, 1977; Wake, 1980; Reilly, 1994). Our observations broaden the hitherto available studies on this topic in the genus *Eurycea* (see Stewart, 1958; Larsen, 1963; Wake, 1966; Sweet, 1977; Mutz & Clemen, 1992) and draw the attention to some sexual dimorphic characters.

Materials and methods

A total of 5 adults of *Eurycea neotenes* (3 females, 2 males) of unknown origin were examined. Specimens that died in captivity were preserved in 70 % ethanol. Total length of males was approximately 68 mm, snout-vent length approximately 33 mm with only a negligible range. The respective measurements in females were 60 mm and 34 mm. Males had three lobes per testis and in females vitellogenesis was in progress or finished. According to Bruce (1976), males therefore were in the third reproductive year or fourth year of life and females were maturing or mature.

Specimens were postfixed in Lillie buffered formalin for 3 days. Cleared specimens were stained only for bone employing the method of Park & Kim (1984).

After drawing, the skeletal structures of the head of the specimens were transferred into an enzyme solution of 30 ml saturated aqueous sodium borate, 70 ml distilled water and 1 g pancreatin for several days to remove the soft tissue. Then the delicate dentigerous bones were extracted, dehydrated in ethanol, critical-point dried and mounted on metal plates. They were sputter-coated with gold and viewed in a SEM (Hitachi S-530).

The length of the head of two males and two females was measured from the midst of the premaxillary arcade to the posterior end of the parasphenoid and from the premaxillae to the condylus. The width of the parasphenoid was determined at the level of the quadrate. Teeth were measured directly on the SEM micrographs.

Results

Length of the male's head was 6 mm from the premaxillae to the posterior end of the parasphenoid and 6.5 mm to the condylus. The largest width of the parasphenoid was 2.2 mm. In the females the head measured 5 mm and 5.5 mm in length, and the parasphenoid 2.0 mm in width.

The upper jaw is composed only of the unpaired (fused) premaxilla. Maxillae are entirely lacking. The tooth bearing *partes dentales* of the premaxillae form only a short arcade. Two long *processus faciales* (*p. praemaxillares* according to Clemen & Greven, 1994) arise

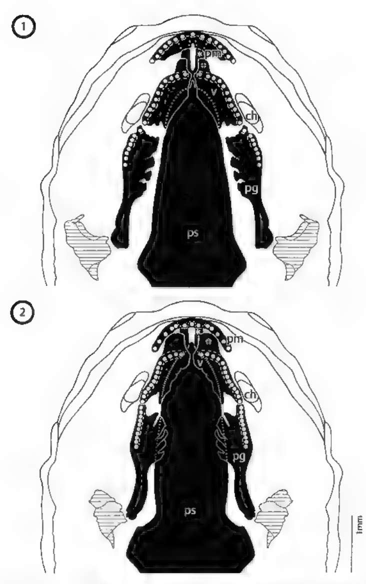


Fig. 1. Ventral view of the anterior part of the skull of an adult female of *Eurycea neotenes* showing the dentigerous and non dentigerous dermal bones of the upper jaw and the palate (black) and the ossified quadrate (hatched). ch, choana, pg, palatopterygoid, pm, premaxillae with anteriorly separated *processus faciales* (*p. praemaxillares*) (asterisk), ps, parasphenoid, v, vomer with anterior process (white point). The posterior portion of the parasphenoid and other cartilaginous and ossified elements of the skull are omitted.

Fig. 2. Ventral view of the anterior part of the skull of an adult male of *Eurycea neotenes*. For further explanations and abbreviations, see fig. 1. Compared with the female (fig. 1), the *pars palatina* of premaxillae (pm) is missing, the *processus faciales* (asterisks) are separated along their entire length, the vomers possess larger anterior processes (white point) and the fissured inner margins of the dentated parts of the palatopterygoid (pg) overlap the broad parasphenoid (ps).

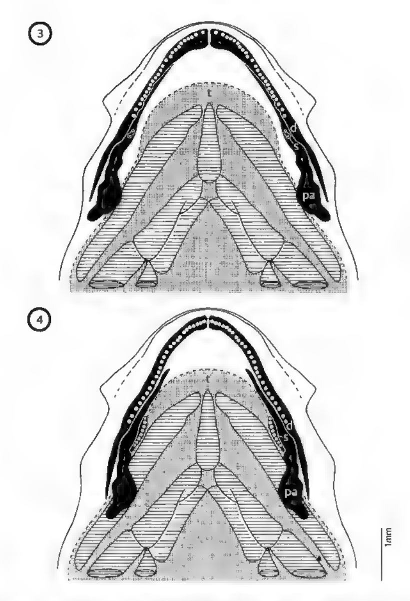


Fig. 3. – Dorsal view of the dentigerous and non dentigerous dermal bones of the lower jaw (black) and parts of the mostly cartilaginous hyobranchial apparatus (hatched) of an adult female of *Eurycea neotenes*. d, dentary; par, prearticular; s, splenial, t, tongue.

Fig. 4. – Dorsal view of the lower jaw (black) and parts of the hyobranchial apparatus (hatched) of an adult male of *Eurycea neotenes*. For further explanations and abbreviations, see fig. 2. Compared with the female (fig. 3), the splenials (s) are larger and the anterior portions of the dentaries (d) are smaller.

immediately below the tooth bearing portion (fig. 1-2). Two third of these processes are fused posteriorly in females; in males they are separated for their entire length (fig 5-6) The toothless bony ledge along the lingual side (*pars palatina*) of the premaxillae is relatively large in females, but absent in males (fig. 1-2).

The ventral components of the skull include fully ossified paired vomers anteriorly and a median large parasphenoid posteriorly (fig 1-2) The anteriorly directed processes of the vomers are small in females, but broad in males (fig. 10). In the former they do not attach to the premaxillae, in the latter they do and cover a larger portion of the *processus faciales*.

The posterolateral margin of each vomer forms approximately two thirds of the bony margin of the inner choana The inner toothless *partes palatinae* of the vomer overlap the anterior part of the parasphenoid (fig 7, 10) Vomers are separated widely from each other posteriorly (fig. 1-2). The ossified paired palatopterygoids begin at the posterior margin of the choanae and extend backwards to, but do not articulate with, the inner surface of the ossified quadrate. In one specimen, however, an adhesion to the quadrate was observed on the left side. The inner margin of the palatinal portion of the palatopterygoid is highly fissured in both sexes (see fig 7) This is obviously more pronounced in males, where this region overlaps the broad parasphenoid. In two females the fissured region was not completely ossified on one side, leaving separated bony patches (not pictured).

The lower jaw is composed of the dentaries that both form a broadly rounded arch. The lingual side of the Meckel's cartilage is invested by the prearticular (fig. 3-4). In females, dentaries are broader at their anterior end, the prearticulars extend more anteriorly than in males. A small splenial (coronoid) occurs on the inner margin of each dentary overlying the prearticular, it is very minute in females (fig 8) and longer in males (fig 9)

Premaxillae, dentaries, splenials, vomers and the palatinal portions of the palatopterygoid bear strictly monostichous teeth (fig 2-3, 7, 9-10) Teeth vary considerably in height Tooth height depends on the site of attachment and on sex. Teeth of males are longer than those of females. These differences appear to be most obvious in the most anterior premaxillary teeth In addition, males have more tooth loci at the vomers, the palatinal portions of the palatopterygoids and, in particular, at the splenials (tab 1) The small number of animals examined, however, does not allow further interpretation of the measurements and counts of functional teeth (tab. 1).

Teeth are separated from each other and are slightly recurved towards the esophagus (fig 6, 11) They are similar in form, but decrease gradually in height and size posteriorly Teeth are ankylosed at the jaws in a distinct pleural condition (fig. 11) and at the labial face of the vomers in a slight pleural condition (fig 10). The majority of teeth of the labial face of the palatinal portion of the palatopterygoid is attached horizontally (females) or more or less pleurally (males). Only a few (2-3) posterior teeth in males are attached horizontally (fig. 7, right side), whereas in females some anterior teeth are attached pleurally due to the different decrease of height of the *pars dentalis*.

Each tooth is composed of a monocuspid crown and a pedicel (fig. 5-12). Both elements are connected by collagenous fibres (fig 13). A prominent dividing zone, however, as in most transformed urodelan teeth consisting of a broad lingual and a small labial deepening is

missing (fig. 11-12). Some teeth show resorption pits mainly in the pedicel and signs of wear apically. All teeth have at their lingual base one large opening to the pulp cavity and additional small holes around the base (fig. 7-8, 11).

Discussion

In *Eurycea neotenes*, the developmental state of dentigerous bones and teeth does not progress beyond the larval condition. Similar traits in the tooth systems were found also in other paedomorphic taxa (for review, see Greven,1988; see also Clemen & Greven, 1977, 1988; Greven & Clemen, 1979).

Maxillae, which seem to appear relatively late during ontogeny in plethodontids (Wilder, 1925, Wake, 1966), and processes forming the posterior vomerine tooth patches that are typical for advanced metamorphosed plethodontids (Stewart, 1958, Wake, 1966, Mutz & Clemen, 1992; see fig. 12 in Clemen & Greven, 1994), are completely missing. Both structures are, however, present in transformed *Eurycea neotenes* (see below).

We found no signs of disintegration of the palatopterygoids. This disintegration is considered as one of the key factors indicating the onset of metamorphosis by some authors (Reilly, 1986, 1987, Reilly & Altig, 1996). Obviously the disintegration of the splenials runs parallel to that of the palatopterygoid, but dental laminae of the palatinal portion of the palatopterygoid as well as of the splenials degenerate far earlier, indicating likewise the onset of metamorphosis (Greven & Clemen, 1985; Mutz & Clemen,1992).

The larval condition holds also for the dentition. In our specimens, dentary, premaxillary, vomerine, palatinal and splenial teeth are strictly monostichous. Generally, in early urodelan larvae, at least the palatinal portion of the palatopterygoid and the splenials bear more than one line of teeth, thus possessing tooth patches ("Zahnfelder"). In transforming *Eurycea* species, reduction of the dentition starts with the formation of a monostichous

Fig. 5. – Fused monostichously dentated premaxillae of a female of *Eurycea neotenes* with partially fused *partes faciales*.

Fig. 6. – Fused monostichously dentated premaxillae of a male of *Eurycea neotenes*. The *partes faciales* are separated for their entire length.

Fig. 7. – Vomer (asterisk) and palatinal portion of the palatopterygoid (point) of a male of *Eurycea neotenes*. Note the only slight pleural attachment of teeth and the fissured palatinal portion (arrowhead).

Fig. 8. – The minute splenial of the female of *Eurycea neotenes* bears only one tooth and overlies the prearticular.

Fig. 9. – The splenial of the male of *Eurycea neotenes* is larger having up to eight tooth loci.

Fig. 10. – Vomer of the female of *Eurycea neotenes* with anterior processes (asterisk) and the labiomarginal tooth-line.

Fig. 11. – Distinct lingual dividing zone of vomerine teeth, male of *Eurycea neotenes*. Note the openings to the pulp.

Fig. 12. – Dividing zone of a premaxillary tooth, labial side, male of *Eurycea neotenes*.

Fig. 13. – Collagenous fibers of the labial dividing zone of a dentary tooth, female of *Eurycea neotenes*.

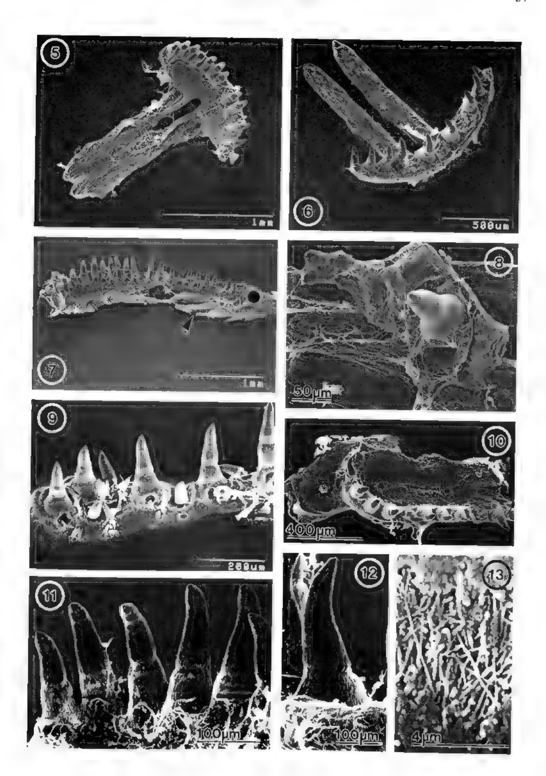

5
1mm
6
500um
7
1mm
8
50µm
9
200um
10
400µm
11
100µm
12
100µm
13
4µm

Table 1. – Height of teeth and number of tooth loci per side in two males and two females of *Eurycea neotenes* as measured on SEM micrographs. Labial height is the distance from the margin of the bone to the tip of the tooth crown, lingual height the distance from the base of the pedicel to the tip of the crown.

Dentigerous bones		Height of teeth in µm		Number of tooth loci (per side)	
		Male	Female	Male	Female
Premaxillae					
Labial	Anterior	325-336	234-254	13-14	14-16
	Posterior	212-245	205-217		
Lingual	Anterior	407-415	325-336		
	Posterior	299-340	387-230		
Vomers					
Labial	Anterior	256-287	227-233	12-14	10-12
	Posterior	228-238	183-190		
Lingual	Anterior	349-354	247-262		
	Posterior	310-315	206-213		
Palatopterygoids					
Labial	Anterior		120-125	9-11	6-8
	Posterior		87-94		
Lingual	Anterior	222-230	175-182		
	Posterior	147-166	138-141		
Dentaries					
Labial	Anterior	248-252	195-203	24-26	23-25
	Posterior	234-241	196-205		
Lingual	Anterior	309-328	308-315		
	Posterior	245-257	219-224		
Splenials		165-205	126-130	7-8	1-2

pattern and ends with the complete disintegration of these bones (WILDER, 1925, MUTZ & CLEMEN, 1992). Therefore monostichy on the palatinal portions of the palatopterygoids and the splenials is regarded as a late larval state. In contrast to other larval urodeles (see CLEMEN & GREVEN, 1977, 1994, GREVEN & CLEMEN, 1985, MUTZ & CLEMEN, 1992, AMEND & GREVEN, 1996), vomerine teeth even of early plethodontid larvae (and paedomorphic plethodontids) hitherto investigated are strictly monostichous (WAKE, 1966, MUTZ & CLEMEN, 1992). Thus, development of the vomerine dentition differs considerably from the general urodelan scheme. Contrary to transformed urodeles, teeth of the vomer and the palatine are ankylosed at the outer (labial) face of the bones, emphasizing again the late larval condition (for review, see CLEMEN & GREVEN, 1994).

Also form and size of the teeth are undoubtedly larval. Teeth are slightly recurved, monocuspid, conical and show a dividing zone that never reaches the condition found in transformed teeth. The typical developmental sequence documented in urodelan teeth is from undivided monocuspid to divided monocuspids in the late-stage larvae to divided bicuspid teeth during or immediately after (partial) metamorphosis (for review, see GREVEN, 1988). Teeth in adult paedomorphic *E. neotenes* therefore can be classified as late larval stage.

Transformed adult plethodontids such as *Eurycea bislineata* (e.g., STEWART, 1958) or *Desmognathus fuscus* (NOBLE, 1931 and further references herein) show a remarkable difference in the premaxillary teeth of males and females. Depending on the testosterone level, males have more elongate and secondarily monocuspid teeth during the breeding period and a subsequent marked loss of these teeth. In addition, males lack the anterior vomerine dentition (NOBLE, 1931). Our few measurements and counts indicate that males of *E. neotenes* have longer teeth, mainly on the premaxillae. Further studies using more specimens captured in different seasons should confirm this observation and help clarify the regulation of this possible sex dimorphism.

Some other obviously sex-linked differences are worth noting. Males also possess broader premaxillae lacking a prominent *pars palatina*, fully separated *processus faciales*, larger anterior processes of the vomer, that overlap the parasphenoid by the fissured margins of the toothless palatinal portion of the palatopterygoid, and large splenials.

According to DUELLMAN & TRUEB (1985: 194), "*Eurycea neotenes* and *Typhlotriton spelaeus* are facultative neotenes intermediate ecologically between obligate neotenes and those species of *Eurycea* that undergo normal metamorphosis in surface waters". *E. neotenes* transforms not only following treatment with thyroxine, but also naturally (for literature see SWEET, 1977). Paedomorphosis, which includes neoteny, however, is evolutionarily fixed (GOULD, 1977). Therefore terms as "obligate paedomorphosis" and "facultative paedomorphosis" should be avoided (REILLY, 1994), but are in common use. As outlined by REILLY (1994), investigations regarding interspeficic heterochrony ("patterns of phyletic change that have become fixed in independent phylogenetic lineages") and intraspecific heterochrony ("variation of individuals in response to environmental change") could help elucidate the paedomorphic state of *E. neotenes*. However, discussion on this is beyond the topic of our paper.

The skull of metamorphosed individuals (see figure 6 in SWEET, 1997) corresponds in most respects to the skull of other transformed *Eurycea* as characterized by WAKE (1966) and MUTZ & CLEMEN (1992). As we studied maturing and mature *E. neotenes*, which reproduced in captivity (HAKER, personal communication), we do not believe that the differences found between sexes should be attributed to different stages of development towards metamorphosis, but reflect real sex specific characters. We do not exclude, however, that an increasing number of breeding cycles (and, thus, briefly elevated thyroxine levels) may enhance metamorphic effects in older specimens as seen on other species (unpublished).

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La larva de *Alsodes gargola* Gallardo, 1970 (Leptodactylidae, Telmatobiinae)

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The tadpole of *Alsodes gargola* is described on the basis of specimens collected at the type locality (Nahuel Huapi National Park and Reserve, Province of Río Negro, Argentina) and nearby areas. The tadpole of *A. gargola* exhibits the diagnostic characters of the genus *Alsodes* (e.g. oral disc not modified, emarginate and with rostral gap; intramarginal mental papillae present; keratodont formula normal, 1:<1>/<1>:2; proctodeal tube present, vent opening dextrally; exotrophic aquatic larvae). The morphology of the tadpoles of this species evidences adaptations to a lotic-benthic habit, a semi-sedentary life, and slow swimming (e.g. depressed body; dorsolateral eyes; ventral oral disc; low fins). Features of the tadpole of *A. gargola* are compared with those of other species of the genus. Remarkable homogeneity exists among morphological characters of known tadpoles of the genus *Alsodes* and those of *A. gargola*. The most striking differences occur between *A. gargola* and *A. nodosus*.

Introducción

El género *Alsodes* contiene 12 especies distribuidas en Argentina y Chile (Lavilla 1992, 1994, Formas, 1995, Formas et al., 1997, 1998). Hasta el presente han sido descriptas las larvas de *A. australis* (Formas et al., 1997), *A. barrioi* (Veloso et al., 1981, Lavilla, 1983, Díaz Pérez, 1984, Díaz & Valencia, 1985), *A. montanus* (Bussi, 1980, Díaz Pérez, 1984), *A. monticola* (Formas, 1975, Lavilla, 1983, Díaz Pérez, 1984, Díaz & Valencia, 1985), *A. nodosus* (Formas, 1975, Bussi, 1980, Lavilla, 1983, Díaz Pérez, 1984, Díaz & Valencia, 1985), *A. pehuenche* (Cei & Roig, 1965, Cei, 1980, Lavilla, 1983), *A. tumultuosus* (Lavilla, 1983, Díaz Pérez, 1984, Díaz & Valencia, 1985) y *A. verrucosus* (Díaz & Núñez, 1988). Las larvas de *A. kaweshkari*, *A. vanzolinii* y *A. vittatus* se desconocen hasta el presente.

Alsodes gargola es una especie endémica del noroeste patagónico, citada hasta el momento sólo para Argentina. Habita cuerpos de agua permanentes lóticos y lénticos en ambientes montañosos hasta los 2000 metros de altitud (Úbeda et al., 1998). Fue descripta por Gallardo (1970) sobre ejemplares colectados en la Laguna Tonchek (41°12'S, 71°30'W,

1750 m) del Cerro Catedral, Parque y Reserva Nacional Nahuel Huapi (Argentina) (fig. 1). GALLARDO (1970) también mencionó algunas características de la larva. Posteriormente, CEI (1976) propuso la existencia de dos subespecies, *A. gargola gargola* para la localidad tipo y *A. gargola neuquensis* para una nueva forma proveniente de la Meseta de Lonco Luan (Provincia del Neuquén, Argentina). CEI (1980) realizó un comentario sobre la morfología externa de la larva de *A. g. neuquensis* y LAVILLA (1983) amplió la descripción de la larva de esta subespecie sobre ejemplares colectados en Primeros Pinos, localidad cercana a la Meseta de Lonco Luan. En el presente trabajo se describe la larva de *A. gargola* (*A. gargola gargola* sensu CEI, 1976) sobre ejemplares provenientes de la localidad tipo y de localidades próximas.

ABREVIATURAS

IZUA: Instituto de Zoología, Universidad Austral de Chile.

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

MATERIALES Y MÉTODOS

Se realizaron muestreos (1996-1998) en cuerpos de agua permanentes, situados tanto en bosques como en ambientes altoandinos del Parque y Reserva Nacional Nahuel Huapi y zonas aledañas. Las localidades de muestreo fueron: Laguna Tonchek en el Cerro Catedral (localidad tipo), Cerro Challhuaco, Valle de los Perdidos, Cerro Carbón y Arroyo Ñireco (Provincia de Río Negro, Argentina) (fig. 1).

Luego de confirmar visualmente la presencia de adultos de *Alsodes gargola* se verificó su identidad específica mediante el reconocimiento de sus caracteres diagnosticos y posteriormente se colectaron larvas con redes de mano. Los ejemplares se fijaron en formalina 10 %, neutra. Algunas larvas se mantuvieron vivas en acuario hasta completar la metamorfosis para verificar su identidad específica, describir la coloración y observar su comportamiento.

Los estadios larvarios se determinaron estableciendo una equivalencia con la tabla propuesta por GOSNER (1960). La descripcion se realizo sobre el analisis de los caracteres morfológicos externos de 28 ejemplares fijados y 10 vivos entre los estadios 27 y 39. Para la morfometria utilizada en la descripción y la tabla 1 se midieron 18 larvas del lote fijado, comprendidas entre los estadios 31 y 36, que en general presentan una constancia en los caracteres morfológicos. Los caracteres cualitativos y el análisis morfometrico se determinaron conforme a LAVILLA (1983, 1988) y LAVILLA & SCROCCHI (1986). Para la nomenclatura de las estructuras córneas bucales se utilizó la presentada por VAN DIJK (1966). La formula dentaria se expresó segun DUBOIS (1995). Las mediciones de los ejemplares se realizaron con calibre de lectura digital (resolución 0.01 mm) y con un ocular con lentilla micrométrica Carl Zeiss (distancia entre lineas 100 μm) incorporado a un microscopio estereoscopico Bausch & Lomb Stereo Zoom 7. Los dibujos fueron realizados con microscopio estereoscopico Leica Wild M3C tipo MTR 31, provisto de cámara clara Wild 308700.

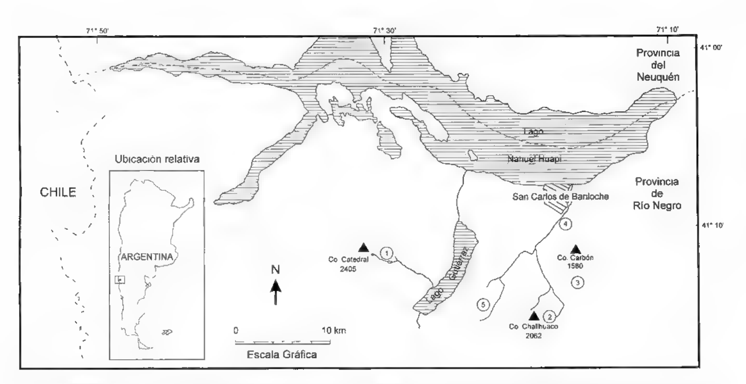


Fig. 1. – Localidades de procedencia del material de *Alsodes gargola* en el Parque y Reserva Nacional Nahuel Huapi (Argentina) y zonas aledañas. (1) Laguna Tonchek, Cerro Catedral, (2) Cerro Challhuaco, (3) Valle de los Perdidos, (4) Cerro Carbon, (5) Arroyo Ñireco. La linea de guiones indica el limite provincial, la linea de guiones y puntos representa el limite internacional. Las alturas de los cerros se expresan en metros sobre el nivel mar.

Las características de la larva de *Alsodes gargola* fueron contrastadas con las que LAVILLA (1988) señaló como diagnósticas para el género *Alsodes*.

Las características larvales de *Alsodes gargola* fueron comparadas con las características de las larvas conocidas de otras especies del género en base a especímenes y/o descripciones publicadas. Se examinaron ejemplares de *A. monticola* colectados en el Lago Espejo (Provincia del Neuquén, Argentina) y de la colección IZUA (1098 A) y material de *A. australis* colectado en el Arroyo Zanjón Hondo (Provincia del Chubut, Argentina) y de la colección IZUA (1629-1630).

Las larvas de *Alsodes gargola* MACN 36787-90 corresponden a los estadios 27, 32, 37 y 39 respectivamente.

DESCRIPCIÓN DE LA LARVA DE *ALSODES GARGOLA* (FIG. 2-3, TAB. 1)

Descripción basada en 38 ejemplares, estadios 27-39, incluidos los cuatro especímenes MACN 36787-90. La larva alcanza gran tamaño (hasta 87 mm, estadio 39). El cuerpo (fig. 2) es deprimido y de forma elíptica en vista dorsal, en vista lateral el contorno ventral es ligeramente convexo; el ancho máximo se encuentra en el tercio medio. El extremo del hocico es redondeado en vista lateral y levemente romo en vista dorsal. Las narinas son circulares, con margenes que presentan un suave reborde de igual nivel en todo su perímetro; se encuentran en posicion dorsolateral y levemente más cerca de los ojos que del extremo del hocico. Los ojos redondos, de mediano tamaño, están en posición dorsolateral, la distancia interocular corresponde aproximadamente a 1/3 del ancho máximo del cuerpo y es similar a la distancia internasal. El tubo espiracular es único e izquierdo, está en posición laterodorsal, separado del cuerpo en su extremo distal y orientado posterodorsalmente. El tubo proctodeal es conspicuo, nace hacia la derecha y se abre en la misma dirección, su abertura puede ser visible dorsalmente. La cola es de mediana longitud (aproximadamente 60 % del largo total), con el eje recto, la musculatura desarrollada y el extremo redondeado; la altura de la cola es algo menor que la altura del cuerpo, las aletas dorsal y ventral son subparalelas entre sí y al eje axial. La aleta dorsal se origina en la unión cola-cuerpo y el nacimiento de la aleta ventral esta enmascarado por el tubo proctodeal.

El disco oral (fig. 3) esta en posición subterminal ventral; su ancho corresponde aproximadamente a la mitad del ancho maximo del cuerpo, es intra-angular (emarginado) y presenta claro rostral cuyo ancho es mayor que la mitad del ancho máximo del disco oral, posee una unica hilera de papilas marginales que en vista dorsal pueden sobresalir del contorno lateral de la cabeza, una hilera de papilas intramarginales mentonianas y papilas laterales en la region supra e infra-angular en numero variable (1-4) o ausente. La fórmula dentaria es 1:<1>/<1> 2; los labios superiores siguen una linea curva y los inferiores una linea recta, los queratodontes son numerosos, los rostrodontes están fuertemente queratinizados y sus bordes libres finamente aserrados, el infrarrostrodonte tiene forma de "V" y el suprarrostrodonte de arco.

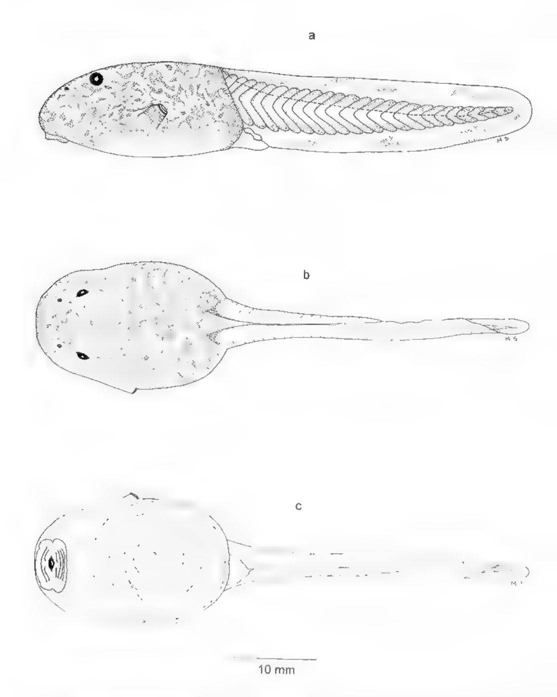


Fig. 2. – Larva de *Alsodes gargola* (MACN 36789, estadio 37, Cerro Challhuaco, 2 marzo 1996): (a) vista lateral; (b) vista dorsal; (c) vista ventral.

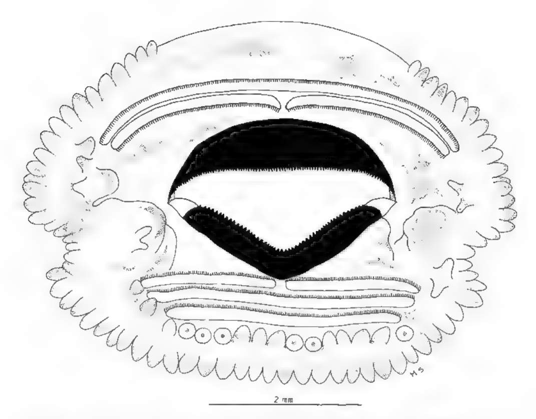


Fig. 3. – Disco oral de la larva de *Alsodes gargola* (MACN 36789, estadio 37, Cerro Challhuaco, 2 marzo 1996)

La coloración de los especímenes vivos es variable, desde negro a castaño claro con manchas irregulares más oscuras y brillos dorados (fig. 2a). El color de la región dorsal del cuerpo presenta la pigmentación mas intensa, alcanzando el negro uniforme (fig. 2b), en tanto que el vientre está menos pigmentado y permite visualizar las asas intestinales (fig. 2c); las narinas y el espiraculo tienen un anillo subterminal negro, el iris es castaño oscuro o negro con un punteado dorado cobrizo, el disco oral muestra la mayor pigmentación en la cara dorsal de las papilas marginales y las estructuras corneas son de color castano oscuro a negro; el tubo proctodeal exhibe una pigmentacion similar a la del vientre, la cola presenta una coloración variable con un patron de manchas mas grandes y nitidas que las del cuerpo, la pigmentación de las aletas es menor que la de la musculatura caudal. Algunos ejemplares tienen una línea vertebral clara que se extiende desde el hocico hasta el tercio medio de la cola, esta línea se conserva en el juvenil y en el adulto. En ejemplares fijados la coloración es castaño grisáceo a gris oscuro, sin manchas ni brillos dorados; el borde de las narinas, del espiráculo y las estructuras córneas varían de negro a castaño oscuro.

Tabla 1. Promedios ± desvíos estándar de las medidas y relaciones morfométricas de la larva de *Alsodes gargola*. Los estadios corresponden a los propuestos por GOSNER (1960). Las medidas están expresadas en mm.

Estadio	31	32	33	34	35	36
Número de ejemplares	5	3	1	2	3	4
Largo total	47,92 ± 4,93	54,45 ± 2,48	43,85	58,68 ± 15,29	57,81 ± 9,54	64,31 ± 8,07
Largo cuerpo	19,87 ± 2,29	22,09 ± 0,84	19,10	22,65 ± 3,70	21,53 ± 1,39	24,39 ± 1,64
Altura máxima cuerpo	9,55 ± 1,40	10,50 ± 1,02	9,57	10,49 ± 0,13	11,03 ± 1,66	12,42 ± 1,48
Altura cola	7,70 ± 1,44	9,32 ± 0,29	7,44	8,62 ± 0,91	8,46 ± 0,60	9,98 ± 1,74
Ancho máximo cuerpo	10,98 ± 1,50	11,56 ± 0,42	11,78	12,61 ± 1,02	12,02 ± 1,52	13,82 ± 1,78
Diámetro ojo	1,50 ± 0,35	1,67 ± 0,23	1,50	1,78 ± 0,18	2,03 ± 0,15	2,12 ± 0,49
Distancia interocular	3,76 ± 0,42	4,16 ± 0,20	3,24	4,27 ± 0,62	4,23 ± 0,25	4,43 ± 0,43
Distancia internasal	3,63 ± 0,66	4,13 ± 0,12	4,10	4,37 ± 0,33	3,87 ± 0,35	4,19 ± 0,14
Distancia narina-hocico	2,62 ± 0,43	2,84 ± 0,26	2,70	3,05 ± 0,92	2,57 ± 0,31	3,30 ± 0,99
Distancia ojo-hocico	5,17 ± 0,68	5,64 ± 0,72	4,90	6,05 ± 2,05	5,30 ± 0,26	6,35 ± 0,95
Distancia espiráculo-hocico	11,16 ± 1,14	12,84 ± 0,91	9,75	12,88 ± 3,23	12,24 ± 1,54	13,92 ± 1,39
Ancho disco oral	5,05 ± 0,38	5,76 ± 0,06	5,49	5,82 ± 0,40	5,75 ± 0,19	6,34 ± 0,38
Ancho claro rostral	3,08 ± 0,19	3,22 ± 0,11	3,32	3,08 ± 0,32	3,39 ± 0,07	3,14 ± 0,35
Largo cuerpo/largo total	0,41 ± 0,02	0,41 ± 0,02	0,44	0,39 ± 0,04	0,38 ± 0,05	0,38 ± 0,02
Ancho máximo cuerpo/altura máxima cuerpo	1,16 ± 0,18	1,11 ± 0,08	1,23	1,20 ± 0,08	1,09 ± 0,05	1,11 ± 0,05
Distancia espiráculo-hocico/largo cuerpo	0,56 ± 0,02	0,58 ± 0,04	0,5[illegible]	0,56 ± 0,05	0,57 ± 0,04	0,57 ± 0,02
Largo cuerpo/altura máxima cuerpo	2,11 ± 0,30	2,11 ± 0,19	2,00	2,16 ± 0,33	1,97 ± 0,21	1,97 ± 0,13
Distancia interocular/distancia internasal	1,05 ± 0,12	1,01 ± 0,05	0,79	0,97 ± 0,07	1,10 ± 0,09	1,06 ± 0,13
Distancia interocular/ancho máximo cuerpo	0,34 ± 0,03	0,36 ± 0,01	0,28	0,34 ± 0,02	0,35 ± 0,02	0,32 ± 0,03
Ancho claro rostral/ancho disco oral	0,61 ± 0,07	0,56 ± 0,02	0,60	0,53 ± 0,09	0,59 ± 0,02	0,49 ± 0,03
Distancia narina-hocico/distancia narina-ojo	1,17 ± 0,17	1,35 ± 0,06	1,23	1,17 ± 0,04	1,22 ± 0,09	1,39 ± 0,43
Distancia hocico-espiráculo/distancia espiráculo-base tubo proctodeal	1,29 ± 0,11	1,40 ± 0,24	1,04	1,31 ± 0,27	1,32 ± 0,21	1,33 ± 0,11

BREVE COMENTARIO SOBRE EL COMPORTAMIENTO DE LA LARVA EN ACUARIO

En acuario, las larvas frecuentan el fondo y las paredes del recipiente. Utilizan las rocas para descansar o encontrar refugio al percibir disturbios y también para alimentarse del epiliton. En el medio artificial las larvas pueden ser alimentadas con pienso escamado para peces de origen vegetal o con carne molida cruda; el alimento es rápidamente detectado. Ocasionalmente se observó a las larvas consumiendo los tejidos blandos de individuos muertos. Las larvas cuando se alimentan varían sus posiciones y movimientos según el sustrato; si se alimentan contra el fondo del recipiente disponen el cuerpo paralelo a éste y realizan movimientos lentos; al alimentarse sobre las paredes, los movimientos son más enérgicos y el cuerpo forma un ángulo agudo con respecto al sustrato. Pueden captar el alimento sobre la superficie del agua colocándose boca arriba y dejando el cuerpo suspendido.

DISCUSIÓN Y CONCLUSIONES

La larva de *Alsodes gargola* presenta las características morfológicas y merísticas (tab. 1) que LAVILLA (1988) reconoció como diagnósticas para el género *Alsodes*: ancho del disco oral menor que los 2/3 del ancho máximo del cuerpo, disco oral emarginado, excepto *A. monticola* y con claro rostral, papilas intramarginales mentonianas, rostrodontes mas anchos que altos; fórmula dentaria 1:<1>/<1> 2, nivel de la abertura de las narinas no elevado; relación entre la distancia narina hocico y narina-ojo > 1, relación entre la distancia hocico-espiráculo y espiráculo-base del tubo proctodeal > 1; espiráculo izquierdo lateral, tubo proctodeal con abertura dextral; aletas de tipo normal; desarrollo larvario acuático y larva con alimentación activa. La larva de *A. gargola* también presenta todas las características que DIAZ (1992) consideró como típicas de las larvas del género *Alsodes* (disco oral > ½ del ancho máximo del cuerpo, áreas comisurales del disco sin papilas, papilas intramarginales mentonianas, relación entre la distancia interocular y la distancia internasal < 1,6) (tab. 1).

La comparación entre la larva de *Alsodes gargola* y las restantes larvas descriptas del género muestra algunas diferencias y similitudes.

Todas las especies descriptas del genero *Alsodes* tienen el disco oral con constricciones angulares, incluyendo a *A. monticola* a diferencia de lo mencionado por LAVILLA (1988). En *A. gargola* el ancho del disco oral es similar a la mitad del ancho máximo del cuerpo al igual que en *A. barrioi*, *A. monticola*, *A. nodosus* y *A. tumultuosus*, en *A. pehuenche* es menor y en *A. verrucosus* es mayor. *Alsodes gargola*, como ocurre con *A. australis*, *A. barrioi*, *A. montanus*, *A. monticola*, *A. tumultuosus*, *A. pehuenche* y *A. verrucosus*, presenta una hilera de papilas intramarginales mentonianas, a diferencia de *A. nodosus* que posee dos hileras de papilas.

La longitud de la cola en relacion con la del cuerpo se presenta con bastante variación dentro del genero, desde 1,2 veces la longitud del cuerpo (*Alsodes barrioi*) a 1,6 veces (*A. australis*, *A. gargola*, *A. montanus* y *A. verrucosus*) y hasta 1,7 a 1,8 veces (*A. monticola*, *A. nodosus* y *A. tumultuosus*). Todas las especies descriptas incluyendo a *A. gargola* tienen el extremo de la cola redondeado, excepto *A. nodosus* que lo tiene suavemente puntiagudo.

Según las descripciones y datos propios, las especies exhiben una coloración similar, excepto *Alsodes barrioi* (Veloso et al., 1981) y *A. monticola* que tienen en el dorso dos manchas irregulares amarillentas a ambos lados de la línea media.

Entre las especies comparadas, la larva de *Alsodes gargola* presenta las mayores diferencias morfológicas externas con la larva de *A. nodosus*, en cuanto al número de hileras de papilas intramarginales mentonianas y a la longitud y la forma del extremo de la cola. En cuanto a la longitud de la cola con respecto al cuerpo, la mayor diferencia la presenta con *A. barrioi*.

La larva descripta en este trabajo (*Alsodes gargola gargola* sensu Cei, 1976) no presenta diferencias en cuanto a la morfología externa y a la coloración con la larva de la subespecie *A. gargola neuquensis*.

De la gran similitud que presentan las características comparadas se pone de manifiesto la remarcada homogeneidad y la constancia generalizada en la mayoría de los caracteres morfológicos externos de las larvas del género *Alsodes*, hecho también señalado por Veloso et al. (1981) y Díaz & Valencia (1985).

Por último, merece destacarse que la descripción de la larva de *Alsodes verrucosus* fue realizada sobre ejemplares provenientes de la Isla Wellington, Chile (Díaz & Nuñez, 1988), donde, según el estado del conocimiento actual, también existen otras dos especies del género, *A. monticola* y *A. kaweshkari* (Grandison, 1961; Formas et al., 1998), no existiendo certeza sobre la asignación específica de esas larvas.

La larva de *Alsodes gargola* por su morfología externa corresponde al tipo "central generalizado" según la clasificación propuesta por Orton (1953) y pertenece al gremio lótico-bentónico (Sección I, B7) según Altig & Johnston (1989). Algunas de las características de la larva como el cuerpo deprimido, los ojos dorsolaterales, el disco oral en posición ventral y las aletas bajas, evidencian adaptaciones al hábito semisedentario y de natación lenta. Todas las larvas descriptas del género *Alsodes* presentan hábitos similares a *A. gargola* y, al igual que ésta, habitan cuerpos de agua permanentes lóticos con lecho de grava y arena, aguas cristalinas y escasa vegetación acuática. *Alsodes pehuenche* también habita cuerpos de agua sulfurosas. *Alsodes gargola* presenta un largo período larvario y metamórfico (Úbeda et al., 1998), característica corroborada en los ejemplares mantenidos en acuario, que superaron los 24 meses de vida como larvas. La etapa larvaria de larga duración es un fenómeno común en otros telmatobiinos.

Resumen

Se describe la larva de *Alsodes gargola* sobre la base de especímenes colectados en la localidad tipo (Parque y Reserva Nacional Nahuel Huapi, provincia de Río Negro, Argentina) y en zonas aledañas. La larva de *A. gargola* presenta los caracteres larvales diagnósticos dados para el género (e.g. disco oral no modificado, emarginado y con claro rostral, papilas intramarginales mentonianas presentes, fórmula de queratodontes normal, 1:<1>/<1>:2, tubo proctodeal presente, con abertura dextral, larva acuática exotrófica). La morfología exhibe adaptaciones al hábito lótico-bentónico y a una vida semisedentaria y de natación lenta (e.g. cuerpo deprimido, ojos dorsolaterales, disco oral ventral, aletas bajas). Se compa-

ran características de la larva de *A. gargola* con las de otras especies del género, poniéndose de manifiesto una remarcada homogeneidad de los caracteres morfológicos. Las principales diferencias se presentan con la larva de *A. nodosus*.

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The tadpoles of *Hyla oliveirai* and *Hyla decipiens* with notes on the *Hyla microcephala* group (Anura, Hylidae)

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The previously unknown tadpole of *Hyla oliveirai* is described and illustrated based on a population from Alagoas State, northeastern Brazil. The tadpole of *Hyla decipiens* is briefly redescribed and illustrated from Rio de Janeiro State, southeastern Brazil, and compared with that of *H. oliveirai*. The latter has a single, wide brown irregular stripe on the tail, while *H. decipiens* has three or four narrower, more regular stripes. The oral disc of both species does not bear denticles and has a single row of papillae extending ventrally and laterally. *Hyla oliveirai* has just one ridge between the beak and the papillae on the lower lip, while *H. decipiens* has two ridges. The tadpoles of *H. oliveirai* and *H. decipiens* are similar to that of *H. berthalutzae* in the general shape, colour pattern and oral disc. These characteristics, added to adult characteristics, may suggest a close relationship between these species. Comparisons between these tadpoles and other species from the *Hyla microcephala* group show remarkable differences, suggesting that *H. oliveirai*, *H. decipiens* and *H. berthalutzae* do not belong in the *H. microcephala* group.

Introduction

The small species of *Hyla* have been arranged into groups by Cochran (1955), Cochran & Goin (1970), Duellman (1970) and Lutz (1973). All of these species that have been studied karyologically have 30 chromosomes (Duellman & Trueb, 1983). The *Hyla microcephala* group is one of these groups and includes small, yellowish-tan species. Highly variable phenetic arrangements have been proposed for this group (e.g., Duellman & Fouquette, 1968, Cochran & Goin, 1970, Bastos & Pombal, 1996). Much of the confusion in these different arrangements has been the result of a lack of knowledge on the osteology, tadpoles, mating calls, and biology of the included species, making it difficult to determine more sharply the relationships among these small hylid frogs.

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As recognized by POMBAL & BASTOS (1998), the *Hyla microcephala* group contains 15 species, seven of them being known from the Atlantic Forest and one from the "cerrado" (sensu AB'SABER, 1977) in Brazil (*H. berthalutzae* Bokermann, 1962, *H. branneri* Cochran, 1948; *H. decipiens* A. Lutz, 1925; *H. haddadi* Bastos & Pombal, 1996; *H. meridiana* Lutz, 1973; *H. oliveirai* Bokermann, 1963, *H. werneri*, Cochran, 1952, and *H. cruzi* Pombal & Bastos, 1998, the latter from the "cerrado"). None of the Brazilian species, except *H. werneri*, were traditionally recognised in the *Hyla microcephala* group (DUELLMAN & FOUQUETTE, 1968; DUELLMAN, 1970).

Hyla oliveirai and *Hyla decipiens* are very similar species with known distribution from northeastern to southeastern Brazil (FROST, 1985; BASTOS & POMBAL, 1996). The tadpole of *H. decipiens* was described, without illustrations, from Rio de Janeiro State by LUTZ (1973). Herein, we describe the tadpole of *H. oliveirai* and compare it to that of *H. decipiens*. Notes about other closely related species are added.

MATERIAL AND METHODS

All specimens examined in this study are deposited in the collection of Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (ZUFRJ). Adults and tadpoles of *H. oliveirai* (ZUFRJ 7326-7328, 7446) were collected from a population in Alagoas State (Município de Quebrangulo, 9°19'S, 36°28'W) in November 1997. Adults and tadpoles of *H. decipiens* (ZUFRJ 4441) were collected from a population in Rio de Janeiro State (Município de Itaguai, 22°44'S, 43°42'W) in March 1991. Coordinates were taken from local maps.

Adults were anaesthetised in 0.25 % chloretone, preserved in 10 % formalin, and stored in 70 % alcohol. Tadpoles were anaesthetised in 0.1 % chloretone and stored in 5 % formalin. Two males and a female of *H. oliveirai* were kept alive and put in a plastic bag where eggs were obtained. The tadpoles that emerged from these eggs were reared until stages 33-37 (GOSNER, 1960) for study. Tadpoles collected in the field were identified by means of comparisons with those obtained from eggs.

The tadpoles of *H. oliveirai* obtained from eggs and others collected in temporary ponds of an open area were raised in captivity in a plastic box (measurements 262 × 77 × 147 mm) with about 1.5 l of water and a dense layer of leaves on the bottom. Eleven tadpoles were maintained in the box. Fish food was regularly provided. The water temperature and pH were not controlled. The studied tadpoles of *H. decipiens* were not raised. However, they were compared with other specimens previously reared by SPCS from the eggs to metamorphosis.

Tadpoles reared from the eggs until stages 36-37 were used in the descriptions and measurements. No changes were observed in the oral morphology or general shape of reared tadpoles. Eventually other stages were used for comparisons and to provide a better account of colour pattern development. Measurements were taken according to the methods proposed by ALTIG (1970) and DUELLMAN (1970), except interorbital distance which was taken between the inner margins of eyes. An ocular micrometer in a stereomicroscope was used for measurements, except for the total length, which was taken with a caliper. Drawings were made using a stereomicroscope with a camera lucida.

RESULTS

HYLA OLIVEIRAI BOKERMANN, 1963 (FIG. 1a-d)

Description. Mean total length at stage 37, 20.7 ± 0.3 mm (*n* = 7, tab. 1). Body oval in lateral view, snout rounded in dorsal view. Body width 65 % (60-70 %) of body length. Eyes lateral, visible ventrally; interorbital distance about twice of eye diameter. Nostrils about six times in eye diameter, rounded, directed ventrally on snout tip. Internostril distance similar to interorbital distance. Spiracle sinistral, short, slightly projecting, distance from spiracle to snout approximately 67 % (60-74 %) of body length. Anal tube short, dextral, attached to ventral fin. Tail length 64 % (62-67 %) of total length, tail musculature tapering gradually to the tip. Dorsal fin starting at final portion of body, slightly arched in lateral view; ventral fin rectilinear in lateral view. Lateral line system invisible. Oral disc anteroventral, its width approximately 23 % (21-27 %) of body width, with single row of rounded papillae extending ventrally and laterally, without denticles; lower lip with one dermal ridge between beak and papillae. Beak strong, finely serrated; upper jaw slightly arched and low jaw approximately U-shaped.

Colour in 5 % formalin. – Body brown in dorsal view, in lateral view with narrow cream stripe extending from snout to lower margin of eye. Body in ventral view brown with marble-like aspect in anterior region and slightly transparent in posterior region. Narrow cream stripes

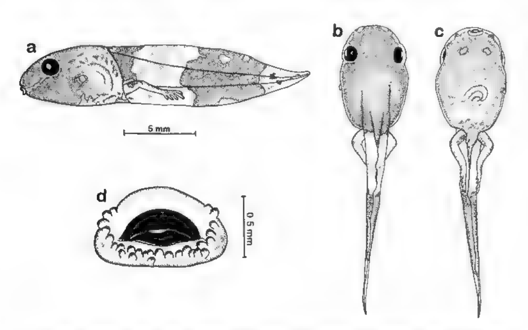


Fig. 1. – *Hyla oliveirai* (ZUFRJ 7446). Tadpole in (a) lateral, (b) dorsal and (c) ventral views, (d) oral disc.

Table 1. – Measurements ($x \pm s$) in millimeters of tadpoles in stage 36-37.

Measurement	*Hyla oliveirai* (n = 7)	*Hyla decipiens* (n = 10)
Total length	20.7 ± 0.3	20.8 ± 0.4
Body length	7.5 ± 0.2	7.7 ± 0.1
Body width	4.9 ± 0.1	4.6 ± 0.1
Body height	4.1 ± 0.1	4.1 ± 0.1
Tail height	4.0 ± 0.1	4.5 ± 0.1
Dorsal fin	1.2 ± 0.1	1,5 ± 0.1
Ventral fin	1.2 ± 0.1	1,4 ± 0.1
Spiracle-snout distance	6.4 ± 0.2	4.5 ± 0.1
Interorbital distance	2.6 ± 0.0	2.5 ± 0.1
Internostril distance	2.5 ± 0.0	2.4 ± 0.0
Eye diameter	1.2 ± 0.0	1.3 ± 0.0
Nostril diameter	0.2 ± 0.0	0.2 ± 0.0
Mouth width	1.1 ± 0.0	1.0 ± 0.0

usually visible on both sides of oral disc, extending to lower margin of eyes in ventral view, forming an inconspicuous inverted "V". Two rounded, slight cream to yellowish-brown depressions under mouth between eyes. Tip of spiracle cream Tail in lateral view cream to yellowish with base of dorsal fin and tail musculature brown and an irregular, transverse brown stripe in posterior half on which yellowish spots (usually one on each fin) may be present.

Colour in life. – Tadpoles in life similar to preserved ones, but with more brilliant colours. Iris coppery Newly metamorphosed frog with a nacreous triangle on snout and two broad nacreous bands disposed laterally from posterior margins of eyes to end of body, area between bands with subrectangular, grayish-brown mark enclosing grayish-brown middle line.

Hyla decipiens A. Lutz, 1925 (fig. 2a-d)

Description Mean total length at stage 37, 20.8 ± 0.4 (n = 10, tab. 1). Body width corresponding to 61 % (55-63 %) of body length Tail length approximately 63 % (60-65 %) of total length, tail musculature tapering abruptly to the tip; fins with rectilinear outline. Oral disc with approximately 21 % (17-23 %) of body width, with single row of slightly rounded and short papillae extending ventrally and laterally, papillae considerably attached to the lip, lower lip with two dermal ridges between beak and papillae Otherwise as described above for *Hyla oliveirai*.

Colour in 5 % formalin Body brown in dorsal view, in lateral view with narrow cream stripe extending from snout to lower margin of eye. Body in ventral view brown with marble-like aspect. Distinct, narrow cream stripes visible on both sides of oral disc, extending to lower

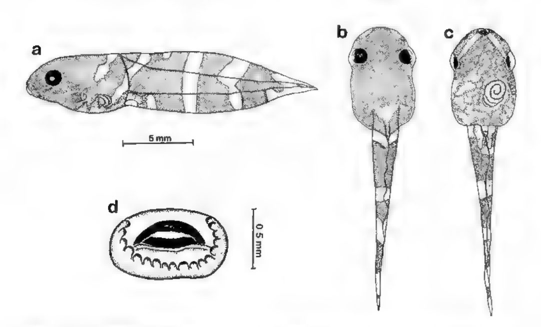


Fig. 2. *Hyla decipiens* (ZUFRJ 4441). Tadpole in (a) lateral, (b) dorsal and (c) ventral views, (d) oral disc.

margin of eyes in ventral view, forming a conspicuous inverted "V". Tip of spiracle cream. Tail in lateral view cream to yellowish with base of dorsal fin and tail musculature brown and three or four irregular, transverse brown stripes.

DISCUSSION

The tadpoles of *Hyla oliveirai* and *Hyla decipiens* have a similar colour pattern and are found in temporary ponds in open areas. Both species present a narrow cream stripe extending from the snout to the lower margin of the eye in lateral view and tail with transversal stripes, alternating brown and cream. They can be distinguished from each other by the number of transverse brown stripes in the tail: one wide stripe with a very irregular outline in *H. oliveirai* and three or four narrower and more regular stripes in *H. decipiens*. The tail narrows gradually in *H. oliveirai*, while it narrows abruptly in *H. decipiens*. The oral disc of both species is similar: reduced, without denticles, and with a single row of papillae extending ventrally and laterally. *Hyla oliveirai* has just one dermal ridge between the beak and the papillae in the lower lip, while *H. decipiens* has two dermal ridges. The papillae in the oral disc of *H. decipiens* are less rounded, shorter and more attached to the lip than in *H. oliveirai*.

The tadpoles of *H. oliveirai* and *H. decipiens* are similar to that of *H. berthalutzae* in the general shape and colour pattern. As in the former two species, the oral disc of the tadpole of

H. berthalutzae lacks denticles and has a single row of papillae extending ventrally and laterally, and two ridges are present between the beak and the papillae in the lower lip (BOKERMANN, 1963). *Hyla berthalutzae* and *H. decipiens*, as well as *H. branneri*, have very similar reproductive habits, although the latter two occur in open areas (LUTZ, 1947; BOKERMANN, 1963; BASTOS & POMBAL, 1996). They deposit the spawn on small dry sticks or leaves hanging above the ponds where the tadpoles will develop. Based on the characteristics of tadpoles, we agree with BASTOS & POMBAL (1996) about the close relationship between *H. oliveirai*, *H. decipiens* and *H. berthalutzae*. According to those authors, it would also be possible to relate *H. haddadi* to these three species based on the adult morphology.

Comparisons between tadpoles of species traditionally included in the *Hyla microcephala* group (see DUELLMAN & FOUQUETTE, 1968; DUELLMAN, 1970) with those of *H. decipiens* and *H. oliveirai* show remarkable differences. The typical tadpole of that group (based on *H. bipunctata* Spix, 1824, *H. meridiana*, H. *microcephala* Cope, 1886, *H. nana* Boulenger, 1889, *H. phlebodes* Stejneger, 1906, *H. rhodopepla* Gunther, 1859 and *H. sanborni* Schmidt, 1944 tadpoles: BOKERMANN, 1963; KENNY, 1969; DUELLMAN, 1970, 1972; LAVILLA, 1990, CRUZ & DIAS, 1991) has an elongate and depressed body in lateral view (ovoid in *H. decipiens* and *H. oliveirai*), eyes almost in the middle of the body length (in the anterior third in *H. decipiens* and *H. oliveirai*), dorsal fin starting at the posterior third of the body (starting at the end of the body in *H. decipiens* and *H. oliveirai*), tail remarkably xiphicercal (just pointed in *H. decipiens* and *H. oliveirai*), and oral disc without papillae and ridges between beak and lower lip (with a single row of papillae and one or two ridges in *H. decipiens* and *H. oliveirai*).

DUELLMAN & TRUEB (1983) assumed that the small hylid frogs with 30 chromosomes form a monophyletic complex, emphasizing that the major evolutionary trends in this complex involve the larval structure, especially the mouthparts. They provided a hypothesis of the cladistic relationships among seven species groups of *Hyla* (*H. labialis* group, *H. columbiana* group, *H. minuta* group, *H. marmorata* group, *H. parviceps* group, *H. leucophyllata* group and *H. microcephala* group). The *H. microcephala* group, previously defined by DUELLMAN (1970), appeared in their study as a monophyletic group with two synapomorphies (both involving larval characteristics): body depressed and labial papillae absent. The remarkable differences (specially those involving oral structure) between the tadpoles of *H. decipiens*, *H. oliveirai* and *H. berthalutzae* and those of the other species traditionally recognized in the *H. microcephala* group suggest that the former ones do not belong to this group.

RESUMÉ

Le têtard de *Hyla oliveirai* est décrit et illustré a partir de spécimens provenant d'une population de l'état d'Alagoas, au nord du Brésil. Un têtard de *Hyla decipiens* provenant du Rio de Janeiro, au sud du Brésil, est brièvement redécrit, illustré, et sa morphologie est comparée avec celle de *H. oliveirai*. Le têtard de *H. oliveirai* a une unique bande marron large et irrégulière sur la queue, tandis que *H. decipiens* a trois ou quatre bandes plus étroites et plus régulières. Le disque oral de ces deux espèces n'a pas de denticules et a une seule rangée ventrale et latérale de papilles. Le têtard de *H. oliveirai* a un seul repli entre le bec et les papilles

sur la lèvre inférieure, tandis que *H. decipiens* en a deux. Les têtards de *H. oliveirai* et de *H. decipiens* sont semblables à ceux de *H. berthalutzae* en ce qui concerne leur forme d'ensemble, leurs couleurs et leur disque oral. Ces caractéristiques, ajoutées à celles des adultes, suggèrent une proche parente entre ces deux espèces. En revanche, la comparaison de ces têtards avec ceux d'autres espèces du groupe de *Hyla microcephala* montre l'existence de nettes différences, suggérant que *H. oliveirai*, *H. decipiens* et *H. berthalutzae* n'appartiennent pas au même groupe que *H. microcephala*.

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Appendix 1

Additional specimens examined

Hyla berthalutzae Bokermann, 1962 – Brazil, Rio de Janeiro State, Municipality of Magé (22°39'S, 43°02'W). Adults: ZUFRJ 2283-2284, 2887, 3137, 5266, 5268-5269, 6613-6619, 6621, 6624-6625, 6628. Tadpoles: ZUFRJ 6629, 7754.

Hyla decipiens A. Lutz, 1925 – Brazil, Rio de Janeiro State, Municipality of Itaguaí (22°44'S, 43°42'W). Adults: ZUFRJ 4463, 4465, 4471, 4475, 4500, 4502, 4506, 4516, 4591-4592, 4594. Tadpoles: ZUFRJ 4543.

Hyla oliveirai Bokermann, 1963. – Brazil, Bahia State, Municipality of Maracás (13°26'S, 40°25'W). Adult: MZUSP 74148

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Euglenoids living in the intestines of microhylid tadpoles of Argentina

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Large numbers of undamaged euglenoids (*Euglena ehrenbergii* var. *baculifera*, *E. spiroides*, *Lepocinclis fusiformis*, *L. salina*, *Phacus curvicauda*, *Trachelomonas bacillifera* var. *minima*, *T. pusilla* and *T. volvocina*) were found in the intestinal contents of tadpoles of *Dermatonotus muelleri* and *Elachistocleis bicolor*. Nine eggs of *Elachistocleis bicolor* were reared in the laboratory in plastic pools until the larvae reached stage 24. Seven of these tadpoles were placed in a glass container with water and a sample of phytoplankton rich in flagellated euglenoids (*Euglena ehrenbergii* var. *baculifera* and *E. intermedia* var. *klebsii*). Two control tadpoles were kept in the absence of euglenoids. Intestinal contents of the tadpoles were observed at stages 25, 27 and 36 (sensu Gosner, 1960). *E. intermedia* var. *klebsii* was found in the intestinal tract of tadpoles of *E. bicolor*. All euglenoids were intact and had typical features of free-living cells in nature, with large accumulations of paramylon granules. We conclude that these euglenoids are not part of the diet of these tadpoles and that they are not digested.

Introduction

Protozoans, algae and nematodes have been reported or suggested as food items in diets of anuran tadpoles (Heyer, 1973; Inger, 1986). Most diet studies have been based on the taxonomic composition of items found in the intestinal contents of fixed specimens. We have found large numbers of euglenoids in the intestines of tadpoles of *Dermatonotus muelleri* and *Elachistocleis bicolor* collected in lentic environments from Argentina (unpublished data). These observations led us to study the euglenoid fauna in the larvae of *Elachistocleis bicolor* obtained from eggs developed in our laboratory and fed with freshwater euglenoids.

There are few reports on diet of microhylid tadpoles (Li & Lin, 1935; Savage, 1952; Heyer, 1973; Inger, 1986; Inger et al., 1986, Wang et al., 1989). Almost all microhylid tadpoles lack keratinized mouthparts and are "filter feeding tadpoles, type 2" of Altig & Johnston (1989). Li & Lin (1935) confirmed living euglenoids in the intestines of *Kaloula*

borealis and commented on the relationship between the protozoa and the tadpoles. Living euglenoids can survive passage through the intestines (HEGNER, 1926). LI & LIN (1935) noticed some digestion of euglenoids. *Euglenamorpha* and *Hegneria* are euglenoids that live in the hindgut of tadpoles (BRUMPT & LAVIER, 1924, WENRICH, 1924). The purpose of this paper is to determine whether tadpoles feed on euglenoids present in their intestines.

MATERIALS AND METHODS

Two samples of tadpoles were examined and staged according to GOSNER (1960). The tadpoles have developed mouthparts and functional intestines in all stages used in this study.

Sample A. – Four tadpoles of *Dermatonotus muelleri* (stages 32, 33, 34 and 36) and two tadpoles of *Elachistocleis bicolor* (stages 36 and 38) were collected from different freshwater pools in Santiago del Estero and Misiones provinces. They were fixed in 10 % formalin.

Sample B. – Nine eggs of *Elachistocleis bicolor* from Corrientes province were reared in the laboratory in a plastic pool with water from the environment where they were collected. Water was changed several times during the next seven days until the larvae reached stage 24. Seven of these tadpoles were placed in a glass container with 250 ml water, and 10 ml of phytoplankton rich in euglenoids (*Euglena ehrenbergii* var. *baculifera* and *Euglena intermedia* var. *klebsii*) were added. The remaining two control tadpoles were reared separately in another glass container and were fed with commercial fish food and yeast (*Saccharomyces cerevisiae*). The euglenoids' sample and the tadpoles were maintained at 18°C with a photoperiod of 12:12 LD.

The intestinal contents of all tadpoles were observed at stages 25, 27 and 36, and from 24 hours to 15 days from the beginning of the experiment. Temporary preparations from the foregut, midgut and hindgut (including the cloaca and vent tube) were made and observed by light microscopy. In the temporary preparations, the wall of a small part of the gut was slit and placed on a glass slide, 1-2 drops of water were added, and a cover slip was placed over the material. In sample A, intestinal contents and buccopharyngeal cavities were also analyzed by scanning electron microscopy (SEM). Tadpoles preserved in 10 % formalin were entire critical-point dried, and the intestines were removed and broken over a piece of double-sided tape placed on a microscope stub. The intestinal contents were coated with gold-palladium. A Philips 515 scanning electron microscope, a vacuum evaporator (ION Sputtering Balzers SCD 040) and a critical point dryer (Balzers CPD 030) were used.

In sample B, in vivo observations of the intestinal contents were made. The algae and protists living in the pond water were identified by light microscopy. Two control tadpoles at stage 31, living in the pond, were examined to verify that euglenoids were present in their intestines.

The following bibliography was used for the taxonomic identification of euglenoids: GOJDICS (1953), HUBER-PESTALOZZI (1955), STARMACH (1983) and TELL & CONFORTI (1986).

The eggs of *E. bicolor* were collected with the permission of and under the rules of the Administración de Parques Nacionales.

Table 1. – Euglenoids found in the gut contents of *Dermatonotus muelleri* and *Elachistocleis bicolor* tadpoles. Parts of intestine: 1, foregut; 2, midgut; 3, hindgut and cloaca.

Taxon	Part of intestines			Observations
	1	2	3	
Euglena ehrenbergii var. *baculifera*			+	undamaged
Euglena intermedia var. *klebsii*	+	+	+	alive
Euglena oxyuris	+	+	+	undamaged
Euglena spiroides	+			undamaged
Lepocinclis fusiformis			+	undamaged
Lepocinclis salina		+	+	undamaged
Phacus sp.		+	+	undamaged
Phacus curvicauda			+	undamaged
Trachelomonas bacillifera var. *minima*	+			undamaged
Trachelomonas pusilla	+			undamaged
Trachelomonas volvocina	+		+	undamaged

RESULTS

Intact cells of *Trachelomonas volvocina*, *T. bacillifera* var. *minima* and *T. pusilla* were found in the anterior zone of the intestines of *Dermatonotus muelleri*. *Phacus* sp., *Lepocinclis fusiformis*, *L. salina* and *Trachelomonas volvocina* were found undamaged in the hind gut of fixed tadpoles (sample A) of *D. muelleri* and *Elachistocleis bicolor*. Large numbers of undamaged *Lepocinclis salina*, *L. fusiformis* and *Trachelomonas volvocina* were found in the cloaca. An intact cell was observed inside the lorica of *Trachelomonas volvocina*. *Phacus curvicauda*, *Euglena oxyuris*, *E. ehrenbergii* var. *baculifera*, *Lepocinclis salina* and *L. fusiformis* were found in the posterior part of the intestines of *D. muelleri*. All euglenoids showed an accumulation of paramylon granules. *E. ehrenbergii* var. *baculifera* also contained many carotenoid granules irregularly distributed throughout the cell. SEM observations of the intestinal contents and buccopharyngeal cavities of the tadpoles confirmed the euglenoid taxa identified with light microscopy. *Phacus* sp., *Trachelomonas* sp. and *Euglena spiroides* were observed in the roof of the buccopharyngeal cavity of *Dermatonotus muelleri* (fig. 1a-b). Intact euglenoids were found along with other protists in the anterior and mid-zone of the tadpole intestines. All these cells were undamaged (fig. 1c-d) and they had typical features of free-living cells in nature (fig. 2a-c). Euglenoids were the only cells that were identified from the hindgut (fig. 2d, tab. 1). Living *Euglena intermedia* var. *klebsii* and other algae (species of

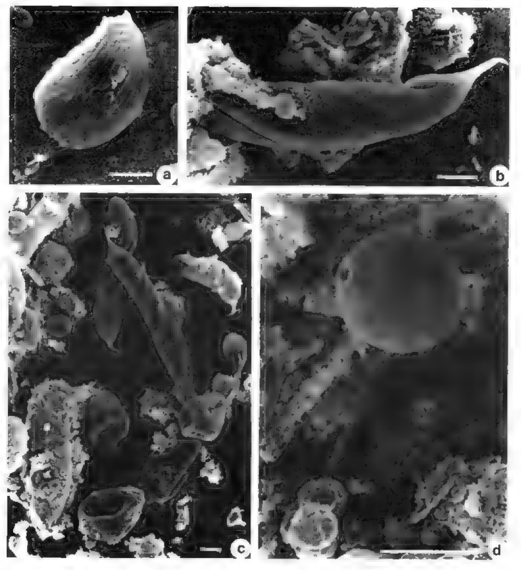


Fig. 1. – (a) *Phacus* sp. on the wall of the buccopharyngeal cavity of *Dermatonotus muelleri*. Scale line, 10 µm (1550 ×). (b) *Euglena spiroides* in the buccopharyngeal cavity of *D. muelleri*. Scale line, 10 µm (1200 ×). (c) SEM view of several euglenoids in the foregut of *D. muelleri*. Scale line, 10 µm (50 ×). (d) *Trachelomonas pusilla* and several dinoflagellates (*Peridinium* sp.) from the midgut of *D. muelleri*. Scale line, 10 µm (3100 ×).

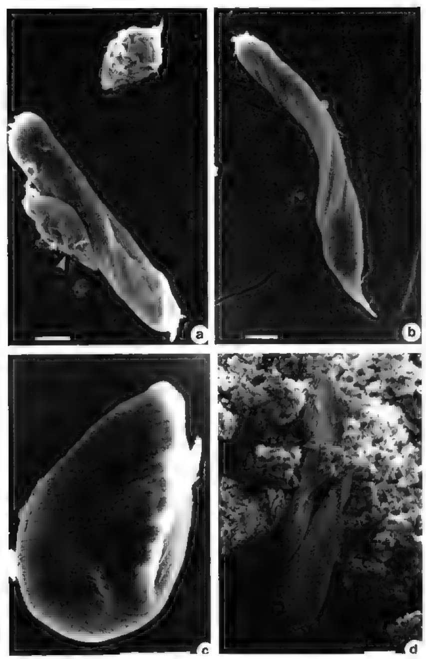


Fig. 2. (a) *Phacus* sp. (arrow) on *Euglena oxyuris* and a contracted *Euglena* sp. from the foregut of *D. muelleri*. Scale line 10 µm (1000 ×). (b) *Euglena spiroides* from the foregut of *D. muelleri*. Scale line 10 µm (1000 ×). (c) *Lepocinclis salina* from the midgut of *Elachistocleis bicolor*. Scale line 10 µm (2400 ×). (d) *Euglena oxyuris* in the hindgut of *D. muelleri*. Scale line, 10 µm. (1000 ×)

Chlorophyceae: *Scenedesmus* sp. and *Ankistrodesmus* sp.; Dinophyceae. *Peridinium* sp.; and Bacillarophyceae: *Nitzschia* sp.) were observed in the foregut and midgut of *Elachistocleis bicolor* (sample B). Only *E. intermedia* var. *klebsii* was found in the hindgut and cloaca. No algae were found in the cloaca other than the living euglenoids. These results were obtained 48 hours, 72 hours and 12 days after the freshwater sample was added to the containers with the tadpoles. The euglenoids were very active, moving inside the intestine, especially in the mid and hindgut, and they occurred in groups over the intestine walls. The intestinal contents of one tadpole of sample B was analyzed 24 hours after placement in the glass container with the phytoplankton. No evidence of *E. ehrenbergii* var. *baculifera* and *E. intermedia* var. *klebsii* were found.

Intestinal contents of four control tadpoles were observed. Two tadpoles were fixed immediately after collection (pond control) from the pond where the eggs of *Elachistocleis bicolor* were obtained. *Euglena spiroides*, *Phacus* sp. and several species of *Trachelomonas* sp. were observed in their intestinal contents. Two embryos were separated from the nine eggs and kept in the absence of euglenoids (intestinal control). Ten days after the experiment began, no euglenoids were observed in the intestinal contents of the developing tadpoles.

Discussion

Although we found euglenoids in the intestines of the tadpoles of *Dermatonotus muelleri* and *Elachistocleis bicolor*, these protists were not digested by the tadpoles of *E. bicolor*. They were alive and intact inside the length of the intestines. This conclusion specifically applies to *D. muelleri* because all individual euglenoids examined with SEM were undamaged. These tadpoles could be non-selective of the kind of organisms they ingest or digest, which agrees with Carothers & Jaksic (1984). A few authors considered euglenoids to be part of the diet of microhylid tadpoles, but the ability of a given tadpole to use euglenoids as food may be determined by whether the tadpole has a gut laminarase that can degrade paramylon granules (Bull & Chesters, 1966, fide Walne & Kivic, 1990). Euglenoids in *E. bicolor* had an excess of paramylon granules, which suggests that the protists stored paramylon, and the intestines did not limit nutrient availability. This agrees with Conforti (1998) and her results of the study on euglenoids' development in an environment with organic enrichment. Tadpoles are microphagous feeders and the size of *Euglena* is within the range of ingested food particles, but the pellicle and the lorica could be an impediment to digestion. Tadpoles have a non-acid intestinal pH and a long intestine with weak peristalsis (Thrall, 1972, fide Altig & Johnston, 1989). Several enzymes were detected in the intestines of microhylid larvae (Altig & McDearman, 1975), but euglenoids seem not to be affected by the internal gut conditions. Euglenoids in the intestines had features typical of cells in samples from the field, including pigmented plastids. These features are probably only possible in lighted conditions. The ventral body wall of these tadpoles is translucent, at least in stages 25 to 31, and few coils of the intestines can be seen through the body wall. We presume that sufficient light to promote growth in the protozoa can pass through the tadpole tissues. The large size of paramylon granules indicates that the level of light and nutrients in the intestines provides favorable conditions for the euglenoids. Large accumulations of carotenoid granules in euglenoids were

reported by BOROWITZKA (1988) as a signal of nitrogen deprivation *Euglena ehrenbergii* var *baculifera* in the intestinal contents of *D. muelleri* had a great number of carotenoid granules in the cytoplasm (this was not in the case in *E. bicolor*).

The number of euglenoids present in the last part of the intestines of *D muelleri* and *E bicolor* tadpoles suggests that euglenoids could enter the intestines via tadpole's vent tube. The vent tube (and the cloaca) have no muscles nearby. A fecal strand usually extends outside the body and could attract protists inside the cloaca *Euglena ehrenbergii* may be able to locate the fecal strands by chemoreception of a particular substance, for example, the nitrogenous wastes of *E bicolor* metabolism Once inside the intestines, euglenoids could move along the short and transparent intestines coils. In sample B of *E. bicolor*, *Euglena erhrenbergii* var. *baculifera* was absent and only *Euglena intermedia* var. *klebsii* was present. The absence of *E. erhenbergii* var *baculifera* could be related to its size and/or its ecomorphological type *E. erhenbergii* var. *baculifera* (188-198 × 19.8-20 µm) is longer than *E. intermedia* var. *klebsii* (78-90 × 7-15 µm) Smaller euglenoids may be more effectively captured by the branchial structures than larger ones, or *E. erhenbergii* var *baculifera* may not be harvested by these suspension-feeding tadpoles because of its benthic habitat. The results of our in vivo study provide new information on the diet of two filter feeding tadpoles of Argentina.

CONCLUSIONS

(1) Euglenoids, along with other algae (several species of Chlorophyceae, Dinophyceae and Bacillariophyceae) were found alive and undamaged in the intestinal contents examined by optical microscopy.

(2) At least the observed euglenoids are not digested because they were always found intact and alive inside the gut (anterior, posterior and cloacal portions). Euglenoid flagellates were the only protists found living in the cloaca.

(3) The storage of paramylon granules in euglenoids suggests that the intestinal conditions were favorable for these organisms, and that they encountered no nutrient limitation

(4) The presence of live, undamaged euglenoids indicates that they are not part of the diet of these tadpoles.

RÉSUMÉ

Dans le contenu intestinal de têtards de *Dermatonotus muelleri* et de *Elachistocleis bicolor* provenant de divers environnements aquatiques, nous avons trouvé une grande quantité d'euglénoides flagellés (*Euglena ehrenbergii* var *baculifera*, *E spiroides*, *Lepocinclis fusiformis*, *L. salina*, *Phacus curvicauda*, *Trachelomonas bacillifera* var. *minima*, *T pusilla* et *T volvocina*) Au laboratoire, 9 oeufs de *Elachistocleis bicolor*, récoltés dans des environnements naturels, se sont développes jusqu'au stade 24 (selon GOSNER, 1980). Les têtards ont été alimentés avec du phytoplancton très riche en euglenoïdes flagelles qui contenait *Euglena intermedia* var. *klebsii*

et *Euglena ehrenbergii* var *baculifera*. Après 48 h, 72 h et 12 jours, nous avons enregistré la présence de *E. intermedia* var *klebsii* vivante à l'intérieur de l'intestin Etant donné que les plastides étaient intacts et que les corps de paramylon étaient similaires à ceux qu'on trouve dans la nature, les algues ne semblent pas affectées par le milieu intérieur de l'intestin. Ces résultats nous permettent de conclure que les eugléno\ides étudiés ne font pas partie du régime alimentaire des larves de ces Microhylidés et supportent sans problème apparent les conditions internes de la cavité intestinale.

Resumen

En el contenido intestinal de renacuajos de *Dermatonotus muelleri* y de *Elachistocleis bicolor* hallamos gran acumulación de euglenoideos flagelados (*Euglena ehrembergii* var *baculifera*, *E. oxyuris*, *E spiroides*, *Lepocinclis fusiformis*, *L. salina*, *Phacus curvicauda*, *Trachelomonas bacullifera* var. *minima*, *T pusilla* and *T. volvocina*), provenientes de distintos cuerpos de agua. En el laboratorio, se dejaron desarrollar 9 huevos de *Elachistocleis bicolor*, recogidos en ambientes naturales, hasta el estadio 24 (según Gosner, 1980) Los renacuajos fueron alimentados con fitoplancton muy rico en euglenoideos flagelados que contenia principalmente *Euglena intermedia* var. *klebsii* y *E ehrembergii* var, *baculifera*. A las 48 horas, 72 horas y 12 días se registró la presencia de *E intermedia* var. *klebsii*, vivas en el interior del intestino. Ellas no mostraron signos de ser afectadas por el medio interno del intestino ya que presentaron los plástidos intactos y cuerpos de paramilon similares a los hallados en la naturaleza Nuestros resultados permiten concluir que los euglenoideos estudiados no formarian parte de la dieta de los renacuajos de microhylidos mencionados, y que soportan sin perjuicio aparente las condiciones internas de la cavidad intestinal.

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A landmark publication on the amphibians of northern Eurasia

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Sergius L. Kuzmin. ***The amphibians of the former Soviet Union***. Sofia, Bulgaria, Pensoft Publishers, 1999: 1-538. $98.00 (US). Hardbound. ISBN-954-642-045-X

In the early 1990's, I was contacted by Kraig Adler of Cornell University to see if I would be interested in working with a Russian colleague on a book on the status of amphibians in the territory of the recently dissolved Soviet Union. I did not know Sergius Kuzmin at that time, and I only reluctantly agreed in order to learn more about the amphibians of that vast territory which until recently had been *terra incognita* to most western batrachologists. Our collaboration proceeded harmoniously, however, and we eventually co-edited a series of publications on the amphibians of Russia and the countries making up the former Soviet Union (Kuzmin et al., 1995, Kuzmin & Dodd, 1996, 1997).

During the course of our collaboration, Sergius asked me to help edit another venture, a book on the biology of the amphibians of the former Soviet Union. Previous field guides on Soviet herpetology were badly out-of-date. In addition, because of the language barriers and the difficulty in obtaining references, much of the primary literature was inaccessible to scientists outside of Russia and the 14 other present-day countries comprising the former Soviet Union. In order to fill this vacuum, he had written a German-language book entitled *Die Amphibien Rußlands und angrenzender Gebiete* (1995), and he hoped to publish an English version to further reach scientists in the West. The original English language edition was never published, although the work was completed in the mid-1990's. Perhaps that was just as well. The present book, greatly expanded from the original version, contains a wealth of information on nearly every aspect of the biology and life history of the 41 species now known from the Baltic Sea to the Russian Far East, from Siberia to the high mountains and deserts of Kazakhstan. This is truly a remarkable work.

The book is organized into chapters as follows: Chapter 1, *History*, Chapter 2, *Faunistics and geography*, Chapter 3, *Ecology*, Chapter 4, *Anthropogenic pressure and conservation*, and Chapter 5, *Keys for species identification*. Chapter 6 is actually a series of detailed accounts for all 41 species of amphibians found throughout the northern Eurasian continent; this section, comprising 300 pages, makes up the greatest part of the book. The book has 65 pages of references covering hundreds of articles. Titles in Russian or other languages of the former Soviet Union (e.g., Georgian, Azerbaijanian) are translated into English. Maps of habitats, species richness and amphibian distributions (based on an atlas grid) are followed by color plates showing habitats and species, including multiple life-history stages, a glossary of terms, species and subject indexes, and a list of species and subspecies with their original authors. Although the color plates are sequestered at the end of the book, black and white photos are liberally placed throughout the main body of the text, especially in the species accounts.

In the *Preface*, Kuzmin describes the purpose of the book (i.e., a state-of-the art rendering of Soviet batrachology in such a manner as to introduce non-Soviet scientists to the literature and scope of research on amphibians) in order to set the stage for the information that follows. He provides line drawings and

descriptions of the morphology of both adult and larval amphibians. These serve as a guide to morphological nomenclature and to the methods by which amphibian measurements are presented in the text (e.g., salamanders were measured from the snout to the anterior portion of the vent). Chapter 1 outlines the history of amphibian research in Russia, beginning with folk legends and paleo-art and extending through the great explorations of Pallas and Kessler, to the foundations of modern amphibian studies, that is, the works of Strauch, Nikolsky and Terentjev. The chapter concludes with a summary of modern amphibian research throughout Russia and the former Soviet Union; this section is invaluable to western researchers as a guide to the extent of amphibian research currently underway and who is conducting it. The history of herpetological research is usually passed over superficially in regional or national texts as various researchers' publications and contributions are discussed. I often wonder about who these people were, what motivated them to chase amphibians at times of great difficulties in travel and social upheavals. After reading Chapter 1, I wish I had the language skills to read some of the biographies available on Russian herpetologists (e.g., MAZURMOVICH, 1983), especially those working during and in the decades immediately after World War II.

Chapter 2 accords an extensive review of biogeography, faunal assemblages and habitat types throughout northern Eurasia. I found this section somewhat tedious, with lists and lists of cold northern habitats and the species that live within them. KUZMIN documents long-term changes in distribution patterns with explanations of how species can disperse or populations can be extirpated in rather short periods of time. He generally rejects rapid dispersion as accounting for new distribution records in favor of an explanation involving the discovery of relictual populations. Such an explanation seems reasonable, although later in the species accounts he notes some rather dramatic range expansions associated with human activity, such as the expansion of *Rana ridibunda* in southern European Russia and Kazakhstan.

Chapter 3 summarizes general amphibian ecology, from activity cycles and reproduction to feeding (Kuzmin's particular specialty) and population structuring. As a semi-tropical resident, I found this section interesting because of its discussion of life histories in, of necessity, extremely cold climates. The diverse ways in which amphibians complete the vital functions of growth and reproduction in a short period of time in a cold climate often mirror the ways they adapt to an unstable (in terms of hydroperiod and seasonal breeding patterns) subtropical environment. Similar developmental and life history plasticity sometimes occur in response to northern cold and subtropical drought, despite our differences in temperature. For example, amphibians living in unstable or extreme environments in Russia and Florida both respond to stress by a decrease in the length of the larval period, and salamandrids in both regions sometimes remain neotenic, when hydroperiods permit, in order to take advantage of favorable feeding and thermal conditions.

I was intrigued by KUZMIN's assertion that "the duration of active life probably is genetically determined to a greater extent than the total life span which includes inactive periods of hibernation". If this is true, would not northern populations of a species live longer than more southern populations? Unfortunately, the lack of references to empirical data impedes examination of this hypothesis (see below). I was also intrigued to learn that exceptionally large larval *Rana ridibunda* become sexually mature after overwintering and prior to metamorphosis. Perhaps gonads could enlarge prior to metamorphosis, but to say that such tadpoles are truly "sexually mature" indicates imprecise terminology (R. ALTIG, personal communication). In any case, endocrinologists and evolutionary biologists should be interested in a frog that develops a mature hormonal system, in part, prior to metamorphosis and when breeding is impossible.

In Chapter 4, KUZMIN presents information on the general status of amphibians in the former Soviet Union. As in most of the industrialized world, habitat destruction and alteration have led to localized declines, and habitat loss has a potential for greatest impact in regions containing species of limited distribution. In addition, collection for pets and teaching, the ubiquitous presence of pollution and toxic chemicals, highway mortality, and the general litany of the ills of modern society have substantially impacted many species, especially now that legal protection has eroded as a result of a lack of enforcement due to a crumbling economic situation. Declines do not seem to be mysterious, as they have been represented in North and Central America and Australia, nor, surprisingly, does disease appear to have figured prominently in declines. Likewise, malformations do not seem widespread, although they occur occasionally, such as in the vicinity of Chernobyl. Because of the remoteness of much of the former Soviet Union and the limited number of amphibian enthusiasts monitoring populations, is the lack of

such reports good news or does it merely reflect sampling bias? KUZMIN provides an extensive review of the conservation of all taxa, including their status in the former republics and their presence in nature reserves. Most species are found in at least a few reserves, except, unfortunately, for the rare salamander *Ranodon sibiricus*. The likely negative effects of extensive social upheaval on the protection and management of the reserves, however, does not invoke cause for optimism.

Chapter 5 is a short chapter devoted to identification. Keys are given not only for mature adults, but also for egg masses and larvae. The keys are accompanied by line drawings of high quality (by N. V. Panteleev), although the lack of color makes distinguishing one gray tadpole from another difficult. Color plates would have greatly enhanced the utility of the keys. Unfortunately, the larvae of some of these species are virtually impossible to distinguish, and there is a great deal of regional color and morphological variation. The numbering system used in the supposedly dichotomous keys is confusing and difficult to follow. I was at a loss in the latter parts of it. Further, there are no drawings of tadpole mouth parts, although these are sometimes used as key characters.

The species accounts are what makes the book invaluable. Nearly everything that one might want to know is covered in depth, at least as far as research in the former Soviet Union is concerned. Each account contains sections on synonymy, names in several languages, taxonomic notes, description, karyology, distribution, subspecific differentiation and variability, ecology (habitats and abundance, thermobiology and activity cycles, reproduction, development, feeding, natural enemies, parasites and diseases), influence of anthropogenic factors, status and conservation, and references (by name and date). The topics are covered comprehensively, and KUZMIN presents alternative points-of-view, such as when describing taxonomic interpretations of the *Rana macrocnemis* complex or the enigma of *Hynobius turkestanicus*. There is a wealth of information here, information which will give Eurasian batrachologists a great deal to ponder in the coming decades (a subterranean *Proteus* in the Crimean Peninsula, perhaps?). In the species accounts, Kuzmin has certainly fulfilled his promise to present the scope of Soviet research on amphibians available to the English-speaking world. The sheer volume of the literature summarized also leads to the book's major flaw, however.

Given the extensive review of the Soviet literature presented by KUZMIN, it is unfortunate that it is impossible to determine the source of information in the text. This is because all literature citations are included at the back of the chapters or species accounts, rather than in the text. Thus, the readers do not know, nor can they determine, whether they are evaluating Kuzmin's personal opinion, the results of his research, or statements based on the empirical research or opinions of others. Fortunately, the tables and some of the figures contain original literature citations. Still, the book would have been much more useful had all the citations been included directly in the text so that the original papers could be connected with the data presented.

There are a few additional problems. For example, a map of the former Soviet Union is presented on page 466; it should have been placed earlier in the book. Although country boundaries are lightly outlined, there are no maps of provinces, districts, or the autonomous republics often mentioned in the text. One not familiar with the geography and political units of Russia, especially, cannot determine where some of the locations referred to in the text are found. The species distribution maps are not labeled at all in terms of place. The text could have been edited better, as there are a number of words that either aren't correct or don't quite make sense (e.g., type "territories" for type localities (p. 2), "semi flowing" waters (meaning streams with only seasonal flow?), "Ecologycal" (p. 43), "fisheries" for hatcheries (p. 382), "forest rides" (?)). The lack of articles (the, a, an) in the Russian language sometimes carries over into the text, and there are a few words (e.g., "synanthropization") that I have never heard of! Still, for such a large work on a complex subject, *The amphibians of the former Soviet Union* is a remarkably easy and enjoyable book to read, especially when compared to most English language works emanating from the former Soviet Union. When the entire book is considered, these criticisms are minor.

The amphibians of the former Soviet Union is a landmark publication in the history of the herpetology of the former Soviet Union, an invaluable reference source, and a much needed compilation of the biology of amphibians across northern Eurasia. It belongs in the library of everyone interested in the biology of Eurasian amphibians, and has much to offer batrachologists throughout the world. I highly recommend it despite the price, which is steep by North American standards. Sergei KUZMIN has provided

the foundation upon which modern studies of the amphibians of this vast territory will be based for a long time to come. Fortunately for biologists fluent in Russian, a Russian language version was issued by the Russian Academy of Sciences in 1999.

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A synthesis of our knowledge about tadpole biology

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Roy W. McDIARMID & Ronald ALTIG (ed.). – ***Tadpoles: the biology of anuran larvae***. Chicago & London, The University of Chicago Press, 1999: i-xiv + 1-444, 115 fig., 27 tables. ISBN 0-226-55762-6.

For a long time, the majority of studies in batrachology were focused on adult morphology or anatomy. Since the last mid-century the increase of our overall knowledge led the researchers to focus their investigations on new research fields or disciplines such as the study of advertisement calls of adult frogs, the study of tadpoles or of ecology and interactions of different species in a population or ecosystem. The numerous studies about tadpoles published during the last decades revealed an extraordinary diversity of forms, modes of development and adaptations to various habitats. All the data published until now, scattered in various periodicals, needed to be compiled in a single book providing a synthesis of available information concerning the biology of anuran larvae. Such a reference textbook should be useful both to the novice and to the confirmed professional. This aim was largely reached by the present book.

This collective book includes a general introduction dealing with the significance of tadpoles in the research world; a glossary which provides accurate redefinition for terms that were more or less currently employed, but whose meaning depended on the author or remained sometimes obscure; an abundant bibliography; an author index, a subject index and a taxonomic index which allow to find easily any theme treated in the book.

Between the introduction and the glossary, the multiple aspects of tadpole biology are divided in eleven chapters. All chapters (including the introduction) have a summary and some provide an exhaustive list of species with the reference to original publications relative to any precise topic. The first one is devoted to the materials and techniques, and review all the herpetologist needs for studying tadpoles, from the collect of these remarkable vertebrates to the scientific material necessary to study them through fixation methods, stage and ecomorphological determination. The four following chapters are relative to general organization of tadpoles. The first of them is devoted to the external morphology of tadpoles, with an emphasis on the oral apparatus morphology and a discussion about functional and evolutionary aspects of tadpole morphology. The last three chapter deal with tadpoles' internal organisation and gather together rare and scattered data about cranial and axial musculoskeleton, viscera and endocrines, and nervous and sensory systems.

An entire chaper is devoted to all cases of endotrophy in anurans (six among the 21 developmental guilds defined by ALTIG & JOHNSTON, 1989), certainly the most peculiar and captivating evolutionary mechanism in Anura.

The last part of this volume deals with the relations of anuran larvae with their environment throughout four chapters. The aspects of physiology of tadpoles treated are those relevant to their ecology, such as respiration, thermal relations, and ion and water balance. Two closely related chapters

gather information about intra- and interspecific relations, social behavior, the repartition of species in the multiple microhabitats available in a biotope, resource use and predation.

The problem of the maintenance and evolution of complex life cycles in anurans first developed by WASSERSUG (1974, 1975) is then discussed in the last but one chapter.

The twelfth and last chapter intends to show the diversity of anuran larvae and gives the most obvious characteristics (geographic range, ecomorphological guild and gross morphological features of oral disk, vent, spiracle, colour and pattern, snout-vent length, and finally authors of the information) for each family and each genus. An illustration is given for certain genera. This overall panorama is completed by a key which helps to find the identification of an unknow tadpole at the family or subfamily level.

The compilation work done by the different authors is considerable, the presentation is very meticulous and illustrations are of excellent quality. Inevitably some lacunae appear when attempts are made for providing exhaustive lists as for instance in tables 12.2 and 12.3 (chapter 12: 297-298), where a list of misidentified and undetermined tadpoles is given. However this kind of weakness is amply excusable in face of the amount of data to gathered. The systematics adopted by the authors in the chapter dealing with diversity mixes recent classificatory schemes (as for example recognizing the family Megophryidae) with older classifications (as the family Rhacophoridae and its three subfamilies Buergeriinae, Rhacophorinae and Mantellinae). I regret also the scarcity of data about the first stages of ontogeny. The only real criticism that I have do to this book is the lack, in the literature surveyed and cited, of representatives of Asiatic species as well as the omission of several important Asiatic authors and of some of their very useful contributions to the knowledge of the Asiatic herpetology.

In conclusion, this book is very impressive by the amount of data gathered and by the work of the authors who succeeded in treating most aspects of larval anuran biology with clarity and pedagogy. This book establishs itself as a major work for all batrachologists and must have its place in your library beside the henceforth essential DUELLMAN & TRUEB (1985).

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